Restoration of species-rich grasslands on reconstructed river dikes

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"Natuurlijk lokken al die bloemen een rijke insectenwereld. Het kan een heerlijk gedartel zijn, soms even bont en druk als op de veel geprezen Alpenweiden".

Uit: Jac. P. Thijsse, 1938. Onze groote rivieren. Uitgave Verkade's Fabrieken N.V., Zaandam.

In liefdevolle nagedachtenis aan mijn vader, die dit graag nog had willen meemaken,

en aan Hub Clephas die, in de rol van paranimf, te weinig tijd van leven bleek vergund.

Stellingen behorende bij het proefschrift 'Restoration of species-rich grasslands on reconstructed river dikes', door Cyril Liebrand.

1. De hoge diversiteit van het landschap in de eerste helft van de twintigste eeuw stond garant voor een spoedig herstel van soortenrijke dijkgraslanden na dijkverbetering. Aan het einde van deze eeuw is de diversiteit van het landschap zover achteruit gegaan dat een natuurlijk herstel van dijkgraslanden na dijkverbetering, zonder hulp van de mens, achterwege blijft.

   "Wanneer ze (dijken, CL) nieuw aangelegd worden of de noodzakelijke verbeteringen ondergaan, dan worden de glooiingen voorzien van een grasmat, hetzij door zodebedekking, hetzij door inzaaiing. Maar het duurt niet lang, of op geschikte plaatsen staat van allerlei moois op." In: Jac. P. Thijsse, 1938. Onze Groote Rivieren. Uitgave Verkade's Fabrieken N.V., Zaandam.

2. Ook voor rivierdijken geldt de uitspraak van Westhoff: "maximale variatie in de ruimte en continuïteit van het beheer in de tijd zijn essentiële voorwaarden voor het behoud van de diversiteit in de natuur". Het terugzetten van de bovengrond en het werken met natuurtechnische beheersplannen draagt hiertoe bij.

3. Flora-verrijkende maatregelen, zoals het uitleggen van maaisel van soortenrijk grasland en inzaai van kruiden dient slechts plaats te vinden met maaisel en zaden afkomstig uit de directe omgeving van het doelgebied. Gebruik van gebiedsvreemd materiaal leidt tot floravervalsing.

   Sýkora, K.V. et al., 1993. Plantengemeenschappen van Nederlandse wegbermen. Uitgeverij KNNV, Utrecht.

4. Soortenrijke dijkgraslanden komen nog maar zo weinig voor dat er alles aan moet worden gedaan om ze te sparen. Deze laatste restanten dienen als ultieme bron voor verspreiding van dier- en plantensoorten naar verbeterde dijktaluds.

   Dit proefschrift.

5. Dijkverbetering is noodzakelijk. Desondanks is er toekomst voor soortenrijke dijkgraslanden met zeldzame (stroomdal)soorten.

   Dit proefschrift.

6. Het beheer na afloop van een dijkverbetering is van essentieel belang voor het ontstaan van soortenrijke dijkgraslanden: dure maatregelen in de aanlegfase zonder een natuurgericht beheer na afloop zijn kapitaalvernietiging.

   Dit proefschrift.

7. Zaadvorming en dispersie zijn van levensbelang voor planten. Een goed maai- of weidebeheer houdt rekening met het tijdstip dat planten zaden produceren.

   Dit proefschrift.

8. Soortenrijke en bloemrijke dijken zijn niet alleen mooi maar ook erosiebestendig.

   Dit proefschrift.

9. Kennis zonder hartstocht is niets anders dan aangeleerde wijsheid.

   Gioconda Belli, 1996. Waslala: Memorial del Futuro. De Geus bv, Breda.

10. Hoe zeer de techniek ook wordt verbeterd, converseren per e-mail wordt nooit 'een goed gesprek'.

11. De vrijheid van het eigen ondernemerschap weegt op tegen de minder zekere financiële toekomst.

ABSTRACT

Liebrand, C.I.J.M. 1999. Restoration of species-rich grasslands on reconstructed river dikes. PhD thesis, Wageningen Agricultural University, Wageningen, 217 pp.

Up until 30 years ago an extensive, flower-rich grassland vegetation containing many species rare in the Netherlands used to be common on Dutch river dikes. However, the deterioration of the flora on dikes was already being reported at the end of the 1960s. At that time too, ecologists warned that the planned reinforcement of the dikes along the Rhine, Waal, Lek and IJssel would adversely affect the flora. Their gloomy forecasts have proved to be correct. Between 1968 and 1992 as much as 89% of the locations with a dry floodplain grassland vegetation in the Netherlands disappeared. In 1992 the vegetation of over 90% of the river dikes consisted of species-poor grassland on which sheep graze, and rough vegetation mown for hay. Only about 7% of the surface area of the river dikes was covered by relatively species-rich grasslands belonging to the phyto-sociological syntaxa *Arrhenatheretum elatioris* and *Lolio-Cynosuretum*, both belonging to the *Arrhenatherion elatioris*. Only 1% was covered by the typical species-rich dry grassland *Medicagini-Avenetum*. The last remnants of these grasslands are in imminent danger of disappearing.

The deterioration in the semi-natural vegetation has mainly been caused by the fact that the slopes of the dikes are increasingly being used agriculturally (fertilization, overgrazing, use of herbicides) but also because ecological features were insufficiently taken into account while reinforcing the dikes. In 1984 a research project was started to ascertain the optimum structure and growing conditions for the grass cover on river dikes (Sýkora & Liebrand, 1987; van der Zee, 1992). The next step was to test the feasibility of the ecological engineering measures proposed in the above mentioned projects empirically. In the research project described in this thesis the core questions were therefore whether the valuable, species-rich vegetation on the dikes can return after reinforcement works, and, if so, what are the pre-conditions for this during and after the reinforcement. The research was carried out on the basis of data of 209 permanent quadrats divided over 125 trial fields. Each permanent quadrat has its own specific method of reconstruction, sowing and management.

Ninety-eight percent of the plant species found before reconstruction, reappeared after reconstruction. Most species reappeared on the replaced former top layer. Only a few (rare) species did not reappear but were still present in the unmodified zone. Most relatively rare species occur only in low numbers and consequently they are still at risk of disappearing, especially if no proper management is applied. Because of this, a spared zone seems to be the best guarantee for the conservation of the plant species after the reconstruction.

In the period 1987-1994 9 plant communities were distinguished within the vegetation of the experimental river dike. They can be classified as follows on the basis of method of reconstruction, management and successional stage: the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) is typical for the spared zone, the species-poor *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) is a rough vegetation resulting from bad management, the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) is a species-rich grassland occurring under good and moderate management practices on replaced sods and replaced topsoil, the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) is an intermediate vegetation which will develop further, either into a hayfield vegetation or into a pasture vegetation, depending on the management applied, the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) is a grassland vegetation strongly influenced by grazing and the *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV), the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII), the fragmentary community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) and the fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) are pioneer stages, which had wholly or almost disappeared in 1994.

The best way to assure maintenance of species-rich grassland vegetation on reconstructed river dikes is to spare a strip or zone of this vegetation during the reconstruction. Species disperse from here to other parts of the dike and the redevelopment of the vegetation is stimulated. To ensure optimal results, the soil composition of those new parts should resemble the soil composition of the spared zone as much as possible. If it is not possible to save part of the original vegetation, the upper soil layer can be set aside in the form of turves or as topsoil and can be replaced as the new topsoil after the reconstruction. Replacing the original topsoil after the reinforcement provides a topsoil of similar composition to that before the reinforcement. Besides, the redevelopment of species-rich grasslands is promoted by previously occurring species re-establishing from the propagules present in the replaced topsoil. The application of the under layer as the new top layer and the use of imported clay as the new top layer both prevent a quick restoration of botanically valuable, semi-natural, species-rich grasslands. Propagules are very rare or even absent.

The seed mixtures applied influence the development of succession. Application of seed mixtures gathered locally accelerates succession. Seed mixtures containing a considerable proportion of *Lolium perenne* seeds are unsuitable, as the redevelopment is retarded, especially when applied in the high densities (such as 70 $kg.ha^{-1}$) which used to be common. Sowing an annual grass species like *Lolium multiflorum* or the standard seed mixture D1 in a low density of 20 to 25 $kg.ha^{-1}$ seemed not to retard the development of a species-rich vegetation.

In the first years after reconstruction the influence of the methods of reconstruction and the seed mixtures applied appears to be preponderant. In the first years the structure of the vegetation is quite open and the competition between species is low. When the vegetation closes, competition increases. Subsequently, management of the vegetation can be used as an important means to regulate competition and, consequently, species composition. A species-rich vegetation only develops when managed properly.

On the basis of erosion resistance features like openness of the sward, ground cover, root density and shear resistance, the best management practices appear to be grazing in June in combination with hay-making in September, hay-making in June in combination with grazing in September and hay-making twice a year. In this respect, grazing twice a year, grazing during the whole season, hay-making in September and hay-making in June in combination with mulching in September are moderately effective. Hay-making in June, mulching twice a year, hay-making once every two year, burning and no management are bad management practices.

On the basis of ecological features such as species-richness and number and proportion of rare species, the best management is hay-making twice a year. In this respect, hay-making in June in combination with mulching in September, hay-making in June, hay-making in September and hay-making in June in combination with grazing in September are moderately effective. The other grazing practices, mulching twice a year, hay-making once every two year, burning and no management are bad management practices.

VOORWOORD

Rivierdijken worden in Nederland reeds eeuwen aangelegd en verbeterd. Steeds met het doel om het achterland de noodzakelijke beveiliging tegen overstroming te bieden. Het rivierenlandschap is hierdoor steeds veranderd. In ons dichtbevolkte land met zijn complexe maatschappij staat de beveiliging tegen overstroming natuurlijk nog steeds voorop. Bij de planvorming voor dijkverbeteringen en dijkbeheer dient echter niet louter de veiligheid tegen overstroming centraal te staan, maar moet ook aandacht worden besteed aan de landschappelijke, natuurwetenschappelijke en cultuurhistorische waarden (LNC-waarden) op en rondom de dijken.
In dit onderzoek staat de vraag centraal of het mogelijk is rivierdijken te verzwaren met behoud van natuurwaarden. De begroeiing van de dijktaluds in ons land dient enerzijds ter verhoging van de erosiebestendigheid van de dijktaluds maar kan door de specifieke omstandigheden van de op het zuiden geëxponeerde dijkhellingen bovendien bestaan uit voor Nederland unieke, zeer soortenrijke en bloemrijke graslanden die ook wel stroomdalgraslanden worden genoemd. In deze stroomdalgraslanden komen vaak vele zeldzame plantensoorten voor die elders in Nederland ontbreken.
Eerder onderzoek heeft aangetoond dat de vegetatie van soortenrijke dijkgraslanden in civieltechnisch opzicht niet onderdoet voor een zeer soortenarme grasmat die bestaat uit enkele grassen. Deze sterk gecultiveerde graslanden werden tot voor kort gepropageerd voor de dijktaluds. In vele opzichten voldoen de soortenrijke graslanden zelfs beter aan de waterstaatkundige eisen die aan de begroeiing van dijken worden gesteld. Dit maakt het mogelijk dat ook andere dan alleen de waterschapsbelangen worden betrokken bij de dijkverbeteringsplannen. De LNC-waarden worden in dat geval uitdrukkelijk meegewogen bij het ontwerpen van het uiteindelijke plan.
In dit kader kwam in 1985 de provincie Gelderland met de wens om de planeisen voor natuurtechnische milieubouw op binnentaluds van rivierverbeteringswerken op een proefobject te toetsen. De aanleg en het beheer zouden de belangrijkste aspecten moeten zijn in dit proefobject. De dijkgraaf van het Polderdistrict Groot Maas en Waal bood hiervoor het dijkvak tussen de spoorbrug in Zaltbommel en de Vier Heuvels in de gemeente Rossum aan.
In 1986 besloot de Coördinatiecommissie tot het instellen van een werkgroep die het onderzoek moest gaan begeleiden. Deze werkgroep stond onder voorzitterschap van prof. dr. Sýkora van de Leerstoelgroep Natuurbeheer en Plantenoecologie van de Landbouwuniversiteit en bestond verder uit vertegenwoordigers van Rijkswaterstaat (dienst Water en Milieu), de provincie Gelderland (dienst Landbouw en Landinrichting), het ministerie van Landbouw, Natuurbeheer en Visserij, het polderdistrict Groot Maas en Waal en het met de uitvoering belaste ingenieursbureau Grontmij terwijl prof. dr. Zonderwijk optrad als adviseur.
Hoewel de invloed van de methode van aanleg op de vegetatiesamenstelling van de diverse proefvlakken duidelijk waarneembaar was in de eerste fase van het onderzoek (1987-1990) bleek dat een proefperiode van vier veldseizoenen te kort was om een afdoende bestudering van de ontwikkelingsmogelijkheden te kunnen verrichten. Met name het beheerseffect op de vegetatie-ontwikkeling is in de eerste onderzoeksfase onderbelicht gebleven. Meerjarig vervolgonderzoek bleek daarom gewenst. In de tweede onderzoeksfase (1991-1995) lag het onderzoeksaccent met name op het effect van het beheer op de vegetatiesamenstelling.
Het onderzoek is financieel mogelijk gemaakt door de directie Gelderland en de dienst Weg- en Waterbouwkunde van Rijkswaterstaat en de provincie Gelderland. Het Polderdistrict Groot Maas en Waal verzorgde gedurende de gehele onderzoeksperiode de niet geringe extra kosten van het beheer en onderhoud.
De vakgroep Vegetatiekunde, Plantenoecologie en Onkruidkunde (thans Leerstoelgroep Natuurbeheer en Plantenoecologie) van de Landbouwuniversiteit verzorgde de huisvesting en stelde haar faciliteiten beschikbaar.
Opvallend groot was de belangstelling voor de proef vanuit verschillende invalshoeken, zowel van omwonenden als van diverse, officiële instanties (Rijkswaterstaatsdiensten, diverse waterschappen, milieugroepen, opleidingsinstituten). Naast proefobject bleek de proefdijk ook een uitstekend demonstratie-object te zijn. In de zomermaanden vonden er vele excursies plaats. De grootste sceptici kregen de tijdens de excursie geplukte bloemen mee naar huis; een betere manier om hen te overtuigen van het belang van mooie en tegelijkertijd sterke dijken heb ik sindsdien niet meer bedacht.

Een woord van dank komt op de eerste plaats toe aan het Polderdistrict Groot Maas en Waal. Het Polderdistrict stelde niet alleen een deel van de door hen te beheren dijken beschikbaar voor de proef maar had tevens zitting in de begeleidingscommissie van het onderzoek. In eerste instantie werd het Polderdistrict vertegenwoordigd door de heren Boonstra en Termont, later door Marc Rademaker en Bas de Bruijn, terwijl ook Krijn de Bruijn jarenlang betrokken was bij de uitvoering van de proef.
Speciaal wil ik Karlè Sýkora bedanken voor de prettige en zeer deskundige wijze waarop hij de wetenschappelijke begeleiding heeft verzorgd van het hele proces, vanaf het eerste veldbezoek in 1986 tot en met het schrijven van het concept vele jaren later. Het terugbrengen van een duizendkoppig gedrocht van meer dan vierhonderd pagina's naar een - hopelijk - leesbaar, compact geheel is een hele klus geweest. En natuurlijk kijk ik met prettige herinnering terug naar de vele, leerzame excursies die we samen hebben gemaakt in binnen- en buitenland en die een aangename afwisseling vormden tijdens de lange veldseizoenen. Professor dr. Zonderwijk (thans met emeritaat) dank ik voor zijn inspirerende adviezen tijdens de veldbezoeken en voor het feit dat hij ooit aan de wieg heeft gestaan van het bermen- en dijkenonderzoek.
Bovengenoemde personen maakten allen deel uit van de begeleidingscommissie die onder voorzitterschap stond van Karlè Sýkora. Deze commissie bestond verder uit Hans Spapens (Rijkswaterstaat, directie Gelderland), Gé Spoon en Rob Priester (Provincie Gelderland) en Louis Fliervoet (Adviesgroep Vegetatiebeheer, IKC-NBLF). In de tweede onderzoeksperiode is de begeleidingscommissie uitgebreid met Frans van der Voort en Dick Verbeek (Provincie Gelderland) en met medewerkers van de dienst Weg- en Waterbouwkunde van Rijkswaterstaat. Afwisselend namen Jan-Willem Seijffert, Jan Muijs, Ton van Schayk en Beppie van de Hengel deel aan de vergaderingen en veldbezoeken.
Monte Gardenier, Jaap Blijjenberg en René Siep, allen tijdens de onderzoeksperiode werkzaam bij eerder genoemde vakgroep, hebben vaak geholpen bij allerlei klussen die varieerden van het meten van de bedekkingsgraad van de bodem in het vroege voorjaar met temperaturen van nauwelijks 0 °C tot het op wiersen leggen van het hooi op dagen dat de temperatuur de 30 °C ruimschoots passeerde. Hiervoor mijn hartelijke dank. Friso van der Zee en Hans Sprangers, die zich tijdens de onderzoeksperiode ook bezig hielden met onderzoek op respectievelijk rivier- en zeedijken, dank ik voor hun belangstelling en hun inbreng bij het oplossen van allerlei theoretische en praktische problemen die zich bij een dergelijk ingewikkelde proef altijd voordoen. Herman Klees heeft enkele tekeningen gemaakt en geadviseerd bij enkele andere. Ali Ormel zeg ik dank voor de voortreffelijke wijze waarop zij het onderzoek financieel administreerde.
Het onderzoek was populair bij stagiaires van zowel de Landbouwuniversiteit als de Internationale Agrarische Hogeschool Larenstein in Velp. Van de LUW waren dit achtereenvolgens: Frank van Langevelde, Marein Verbeek, Marcel Gutter en Hein van Kleef, van de IAHL: Gerda Bongertman, Cathy Huynen, Karel Meinen, Herbert Dijkhuizen en Wendy van Kemenade. Zij hebben ervoor gezorgd dat de gebruikelijke eenzaamheid van een veldonderzoeker op prettige wijze werd verstoord.
Twee personen die belangrijk zijn geweest tijdens het onderzoek waren mijn kamergenoten Tim Pelsma en Louis de Nijs. Gesprekken met hen en terloopse opmerkingen hebben vaak de olifanten die op mijn pad kwamen weer teruggebracht tot de normale proporties van een mug. Vooral op de maandag-ochtenden kwamen de relativerende en opbeurende opmerkingen van Tim en Louis vaak goed te pas. Het gezamenlijk afbranden van het proefvak met brandbeheer en het vervolgens heffen van het glas vormde een jaarlijks terugkerend ritueel als start van het veldseizoen.
Vanaf 1996 vond het schrijven van het eindconcept plaats naast de werkzaamheden van mijn adviesbureau EurECO. Ondanks dat ik het werken in de avond- en nachtelijke uren zoveel mogelijk heb beperkt was dit in sommige perioden onvermijdelijk. Nooit heeft mijn grote steun en toeverlaat Charlotte hierover geklaagd. De waarschuwing dat het schrijven van een proefschrift vaak ten koste gaat van je relatie is voor ons van generlei belang geweest.

Tot slot spreek ik de hoop uit dat de resultaten van dit onderzoek ertoe zullen leiden dat we voortaan niet alleen in de verleden tijd over bloeiende dijkhellingen kunnen mijmeren, maar dat ook in de toekomst een langgerekt, kleurrijk lint van bloemrijke dijkgraslanden de toch al populaire fiets- en wandeltochten over de dijken nog meer de moeite waard zal maken.

Cyril Liebrand

Table of contents

Parts of this chapter have been included in the following publications:

Liebrand, C.I.J.M. & K.V. Sýkora, 1992. Restoration of the vegetation of river embankments after reconstruction. In: *Aspects of Applied Biology*, 29, Vegetation management in forestry amenity and conservation areas, pp 249-256. Assoc. of Applied Biologists, Univ. York, England.

Liebrand, C.I.J.M. & K.V. Sýkora, 1996. Restoration of semi-natural, species-rich grasslands on river dikes after reconstruction. *Ecological Engineering*, 7: 315-326.

CHAPTER 1

GENERAL INTRODUCTION

1.1 MOTIVE FOR THE RESEARCH

Deterioration of the vegetation on river dikes

Up until 30 years ago a flower-rich grassland vegetation containing many species rare in the Netherlands used to be common on Dutch river dikes (Neijenhuijs, 1968; Cohen Stuart, 1959; Cohen Stuart & Westhoff, 1963). The first report of deterioration of the flora on dikes was by Neijenhuijs (1969), who suggested that the use of fertilizer, herbicides and pesticides was responsible for the sharp decline in the number of species in this vegetation. At that time too, ecologists warned that the planned reinforcement of the dikes along the Rhine, Waal, Lek and IJssel would adversely affect the flora. They pointed out that it was very uncertain whether the specific dike flora with its many rare species would be able to recolonize the improved dikes, claiming that this would greatly depend on the material used to reinforce the dikes and on the measures taken to spare the existing flora.

The gloomy forecasts of the fate of dike flora proved to be correct. Between 1968 and 1992 as much as 89% of the locations with a dry floodplain grassland vegetation in the Netherlands disappeared (Van der Zee, 1992). At present the vegetation of over 90% of the river dikes is species-poor grassland on which sheep graze, and rough vegetation mown for hay. The deterioration in the semi-natural vegetation has mainly been caused by the slopes of the dikes increasingly being used for agriculture (fertilization, overgrazing, use of herbicides) but also because ecological features were insufficiently taken into account while reinforcing the dikes. A research project on the vegetation development on improved dikes was set up within this context.

The research described in this thesis was stimulated by the growing general interest in the conservation, restoration and development of ecological features in the Dutch landscape, which has largely arisen in response to awareness that nature is deteriorating rapidly in the Netherlands. This deterioration began slowly, so the urgency for a large-scale rescue operation was not initially felt. Of late, however the deterioration and dismantling of the traditional Dutch rural landscape have gained momentum. Nature and landscape conservation societies have therefore been formed, with the aim of preserving the remaining ecological features. This increasing interest in the development and restoration of ecological features is to be welcomed.

1.2 ECOLOGICAL CONSIDERATIONS ABOUT RESTORING PLANT COMMUNITIES

This thesis is a feasibility study of restoring endangered species-rich plant communities on reinforced and reconstructed river dikes. Restoration in this context generally refers to the efforts to reassemble a community or ecosystem and to allow it to function properly (Jordan III *et al.*, 1987). There has been remarkable progress in land restoration technology during the past 35 years (Bradshaw, 1987). There are now many degraded environments in which the original ecosystem or an effective substitute can be re-established. Unfortunately, much of the detailed methodology is available only in special publications, though there are two substantial reviews (Schaller & Sutton, 1978; Bradshaw & Chadwick, 1980). Nevertheless, it should be noted that not all such restoration efforts will always be perfect; many will be at least partly a failure. The products may be deficient in either structure or function. And while a study of how success is achieved is very instructive, it may be even more worthwhile to chart the difficulties and attempt to account for them. Actually restoring the original communities means restoring *diversity, species composition* and *ecosystem function*. The starting point must be the soil, or at least the substrate into which plants must establish and root. Its properties and situation are crucial to the degree to which an ecosystem can develop naturally on the site, how far this development will progress and what treatments are necessary to assist its development. In relation to the maintenance of species richness in plant communities Grubb (1977) introduced the concept of the regeneration niche - the particular environment where a plant begins its development - as a very important part of the overall niche. In the restoration of ecosytems one might suppose that the regeneration niche space would be wide open. But in reality it may lack particular attributes and therefore be unsuitable for most species. The first ecological step is therefore to manipulate the regeneration niche by physical, chemical and biological means, to tailor it appropriately to the species that are wanted. This can only be done properly if the specific requirements of individual species and ecosystems are understood.

The aim of restoration is to accelerate succession. To ensure succession it is necessary to understand the factors limiting succession at each point of its progress and to deactivate them by specific treatment. There is a need to optimize the environment, both for individual species and for the entire ecosystem. This is because both species and ecosystems have specific physical and chemical requirements, which in natural ecosystem development may only be satisfied after some time has passed. As a result, ecosystem restoration provides a way of seeing more clearly the needs of ecosystems and the importance of both allogenic and autogenic factors in (primary) succession. Allogenic factors arise from outside the community, autogenic factors from within it. In particular, the contribution of autogenic factors which can be demonstrated in the course of the restoration work indicates the importance of facilitation, in the sense of Slatyer (1977). This is the idea that one species makes it easier for a second species to participate in a particular succession. Facilitation leads to 'relay floristics', the concept that there is a specific sequence of species (Egler, 1954). One of the most interesting aspects of ecosystem restoration is the practical need to compress establishment into one phase so that relay floristics cannot occur. One instrument to achieve this could be the applied management regime which influences the competition between species, for competition is a critical factor in restoration practice.

One important question is what should be the explicit goals of the restoration. A major goal could be to create starting locations from where appreciated species can then spread to neighbouring areas, thereby accelerating the development of extensive species-rich grasslands. The success of the restoration may be considered by measuring the proportion of *target species* which is achieved after a certain period of time. The target species are based on the ecological potential of a habitat and together they frame a *target vegetation*. The habitat conditions of the target vegetation must be known in order to be able to answer the question of what is the minimum knowledge required to be able to achieve the goals. Although as much knowledge as possible is used to predict the target vegetation, there will always be successful and unsuccessful species. It is difficult to say when a restoration has succeeded and when it has not. Species are considered to have established when they have reached the *minimum viable population* (MVP concept; Gilpin, 1987). This MVP varies greatly for different species. The duration of a restoration activity is considered to be the time required to reach a *dynamic equilibrium* (Cairns, 1987).

Different attributes can act as limiting factors in restoration succession or may hinder the rate of ecosystem development. They may be physical, chemical or biological. One of the most interesting is the biological factor of immigration. The supply of suitable propagules is important in determining ecosystem development on reconstructed river dikes or other degraded land. Where the new substrate of the dikes or the degraded land is alien and very different from the natural soils of the immediate region, it is possible that the ecologically appropriate species are not present in the vicinity. In this situation the only species that will be able to colonize will be those with special powers of long-range dispersal. What is crucial is that the whole process of ecosystem development can be held up by the lack of suitable colonists (Bradshaw, 1983). This can be tested directly by means of sowing experiments in which missing species are deliberately introduced. Species that rapidly spread over the target site clearly show that ecosystem development was being held up by lack of colonists.

The experiments done on restoration fall into one of two groups. The first type essentially involves carrying out some kind of manipulation, making some kind of change in the environment, then stepping back to see what happens (Werner, 1987). Typically, the alterations that are made in these *empirical* experiments are rather gross ones that influence the entire community or ecosytem in some way; running a fire through it, for example, or adding fertilizer. Experiments of this kind are commonplace in ecological restoration and management research because they are relatively easy to carry out. It is important to recognize, however, that this approach essentially black-boxes many things that are going on in the community, treating them as processes for which input and output are understood but the process itself is not understood in any detail. For example, this approach black-boxes all the species interactions, and the specific ways individual species respond to changes in the environment. This may be of great interest to the ecologist and to anyone who is trying to restore a community. The basic weakness of experiments of this kind is that they may provide some information about what works under a given set of conditions, but they say very little or nothing about why it works. This means that it is impossible to extrapolate from these experiments to different situations. The other type of experiment is the experiment designed not simply to demonstrate that a particular manipulation produces a particular result under a given set of conditions, but to provide information about why it gives those results. This *mechanistic* type of experiment usually deals with some specific aspect of a single species or small group of species and the role these play in the community. This may involve some ecosystem function such as nutrient cycling, or it may involve the interaction between several species. It may be carried out on organisms growing alone or in small groups, or even in place in the community; but in either case, the objective is to identify and characterize mechanisms, and to obtain information that will help the ecologist understand why certain things happen in the system. This being the case, it is obvious that there is a need of both kinds of experiments. The rougher, more empirical experiments can help to answer urgent questions as quickly as possible for purely practical reasons, but the more mechanistically oriented experiments are indispensable for providing information that will ultimately allow conservationists to work with confidence under a variety of conditions and even to make appropriate adjustments in those conditions to achieve the desired results.

Restoration of biodiversity has become a major policy goal in the Netherlands (Bal *et al.*, 1995). One of the ecosystems that have a high priority in the Netherlands to be reinstated on sites with good prospects, is the nutrient-poor dry meadow, because this ecosystem has been dwindling rapidly due to eutrophication and mismanagement. In order to be able to restore this ecosystems, it is crucial to analyse three sets of related problems. The first set of problems is related to restoring the growing conditons appropriate for the plant species selected; the *suitability*. The second set deals with the availability of propagules (seeds, fruits, vegetative parts, bulbs); the *accessibility*. The third set of problems contains the *sustainability* of the community. Attention has to be paid to the influence of competition as a critical factor in restoration practice.

1.2.1 Suitability of a target site

Restoration involves ameliorating the habitat quality for the selected plant species by applying the correct counter measures, e.g. by reducing the availability of nutrients to plants to levels that favour the growth of the selected plant species through an appropriate management (Bakker, 1989). Generally, the suitability for species-rich plant communities containing rare species depends primarily on the fertility of the soil. The fertility of the soil is determined by the granular composition and the management of the vegetation. Within the granular composition the clay content plays an important role. However, a low clay content is not a guarantee for a species-rich vegetation, since the management also evidently affects the habitat. Manuring or leaving the cut material leads to accumulation of soil nutrients which raises the above-ground biomass. Consequently, a large above-ground biomass hampers the development of a species-rich vegetation.

The suitability of a target site can be artificially improved by using different restoration techniques. One such technique is to replace the former topsoil in situ, which in the past has proved to be suitable for the establishment of a species-rich vegetation. Sharp transitions between soil layers with different granular composition should be avoided, since roots are often unable to pass through them. It is recommended to use the material of the former topsoil on locations which have a good chance of developing a species-rich vegetation. Seed rain from these parts will cause species to spread to the other parts of the reconstructed dike.

Restoration management

Management is an important tool in the restoration of species-rich grasslands. During the first part of the twentieth century, large areas of semi-natural grasslands and heathlands were brought into agricultural use in Western Europe (Van der Woude *et al.*, 1994). Until the 1950s, the extensive agricultural use of these grasslands resulted in species-rich, but relatively unproductive communities with many characteristic and rare species (Olff, 1994). Since then, agricultural practices have intensified. The much higher fertilizer inputs, lower water tables and higher cutting frequencies and grazing densities have caused these communities to dwindle or even disappear in most areas. Nowadays, many of these areas are being taken out of production and brought under nature conservation management again, with the aim of restoring former species-rich plant communities. The negative relationship between nutrient availability, above-ground biomass production and species richness is widely acknowledged (Grime, 1979; Vermeer & Berendse, 1983; Olff & Bakker, 1991). On eutrophic soils species-rich communities can only be established after nutrient impoverishment until a mesotrophic level has been achieved. Nutrient impoverishment can be achieved by hay-making without manuring or fertilization. Apart from directly affecting the structure of the sward (Bakker, 1987), hay-making influences the nutrient cycle, especially by removing the minerals accumulated in the standing crop (Bradshaw, 1980; Wells, 1980; Oomes, 1990).

It seems feasible to assume that there is a trade-off between competition for nutrients and light (Bakker *et al.*, 1995). Species dominating in early restoration successional stages with superfluous nutrients and high production win the competition for light. Species dominating in late successional stages with an open canopy and superfluous light win the competition for nutrients. Restoration management is accompanied by a dwindling standing crop and an increasing species-richness (Bakker & Olff, 1992).

On the basis of the results of some studies of the effect of restoration management on the biomass production and the diversity (e.g. Oomes & Altena, 1987), Oomes (1988) suggested a general pattern of the process of impoverishment consisting of four stages: 1) productivity decreases after stopping intensive land use with manuring, 2) changing competition between species; fast growing species dwindle and slower growing species increase, 3) production relatively low and canopy relatively open; increase of low-abundant species and germination and establishment of species out of the seed bank, and 4) germination and establishment of species from the neighbourhood that have arrived by dispersion. The soil can be impoverished by hay-making. Soil nutrients, especially nitrogen, phosphorus and potassium, are removed with the hay.

Relation between above-ground biomass and species richness

In general, the highest species richness is found when the peak standing crop including litter is between 3.5 and 7.5 tons $dw.ha^{-1}.yr^{-1}$ (Al-Mufti *et al.*, 1977; Peet *et al.*, 1983). Altena and Oomes deal with annual production and assume a maximum annual production of 5 to 6 ton $dw.ha^{-1}.yr^{-1}$ for species-rich grasslands (Altena & Oomes, 1985; Oomes, 1988, 1990). Bakker (1989) found the highest species diversity (≥ 20 species per 4 m^{-2}) between 2 and 4 ton $dw.ha^{-1}$, which is not in agreement with Grime's optimum of between 5 and 6 ton $dw.ha^{-1}$. Oomes & Mooi (1981; 1989) found that the species diversity did not always increase despite a large decrease of the standing crop. Immigration of species into a stand depends not only on the habitat conditions but also on the reservoir of species in the vicinity. But even if all conditions are optimal, it takes time before the developing vegetation communities are saturated.

Numerous alternative explanations for the effects of productivity on diversity have been proposed. Grime (1973, 1979), for instance, suggested that productive habitats have lower diversity because of more intense competition. Newman (1973) countered that competition is equally strong in both fertile and infertile habitats, but that in productive habitats strong competition for light inherently favors the tallest species, whereas in infertile habitats many alternative traits confer competitive ability for nutrients and thus allow numerous species to coexist. MacArthur & Wilson (1967) suggested that the biodiversity of a site depends on the interplay of local colonization (gain) and extinction (loss) rates. Tilman (1993) supposed that changes in species richness along productivity gradients should depend on the effects of productivity on both the colonization and extinction probabilities of species. In his study, experimental increases in productivity via nitrogen addition generally led to decreased species richness. The decreased diversity was caused as much by lower rates of species gain as by greater rates of loss of existing species. He concluded that diversity is lower in productive grasslands because accumulated litter, and possibly lower light penetration, inhibit germination and/or survival of seedlings, and thus decrease rates of establishment by new species. Higher productivity also leads to higher rates of loss of existing species, presumably via competitive displacement.

Attributes limiting biomass production

Three soil attributes which can limit biomass production are nitrogen, phosphorus and potassium. These elements must be present in a certain ratio to achieve optimal production. Manuring recommendations are usually attuned to these ratios. If one of these elements is deficient, biomass production can be limited. In practice, nitrogen and potassium appear to be the most important limiting elements whereas only in very rare circumstances phosphorus is limiting. Oomes (1988, 1990) contended that on sandy soils the attribute limiting biomass production is potassium and on clayey soils it is nitrogen.

In unmanured grasslands fertility depends on the speed of mineralization of organic matter (Dickinson, 1984; Vaughn *et al.*, 1986). The decomposition of the organic matter greatly depends on the C/N ratio and the moisture content of the soil (Scheffer & Schachtschabel, 1976). Usually, the C/N ratio of soils with stabilized humus is about 10, but values of 8 and 9 are also possible (Janssen & Verveda, 1983). A C/N ratio higher than 12 or 13 indicates a N deficiency in the soil. This retards the humification process and thus the nitrogen mineralization. The C/N ratio of the organic matter in sandy soils is higher than in more clayey soils. On the experimental dike the mean C/N ratio per method of reconstruction never exceeded 12, which means that mineralization was never inhibited. On imported clay this ratio was exactly 12, so here further impoverishment might lead to N deficiency.

1.2.2 Accessibility of a target site

There are two alternative strategies by which plants may spontaneously (re)colonize a target site; either through the germination of seeds from the seed bank available in the soil of the target site or through the dispersal of seeds produced by populations in neighbouring sites (Bakker & Olff, 1992). One of the causes of the decline of species-rich plant communities is the fragmentation of natural and semi-natural habitats (MacArthur & Wilson, 1967; Gilpin & Hanski, 1991; Van Dorp, 1996). An answer to this problem might be the creation of ecological networks (Verboom *et al.*, 1993).

Seed bank

Grime (1979) distinguished four types of seed banks, i.e. (1) transient seed bank with seeds germinating in the autumn immediately after the seed rain, (2) transient seed bank with seeds germinating in the spring after stratification, (3) persistent seed bank with seeds germinating in both autumn and spring and containing a small seed pool during the year and (4) persistent seed bank with seeds germinating in both autumn and spring and containing a large seed pool which doesn't change much with the seasons and is large in relation to the annual production of seeds. In fact, the situation is more complicated, as can be seen from population biology research on different species. For example, Van der Vegte (1978) and Ter Borg (1985) respectively have stated that *Stellaria media* and *Rhinanthus angustifolius* feature both a transient and a persistent seed bank. Most species expected to increase during restoration succession have no long-term persistent seed bank (Bakker *et al.*, 1995) and must therefore be dispersed from elsewhere. Additionally, the probability of seed survival in soil seed banks depends on factors such as the capacity of seeds to remain dormant at various depths in soil and the duration of burial.

Seed dispersal

The probability of seed arriving in a target area depends on factors such as the number of seed sources in the landscape and their distance to a target site, the production of seeds and the presence and efficiency of dispersal vectors such as water, wind, animals and humans (the latter includes machinery, cars, soil redistribution, etc.). So, in situations where soil seed banks have been depleted because of the rapid decay of buried seeds or the removal of the topsoil, seed dispersal is the only natural option to restock a target site with seeds. In general, the establishment of species by natural processes tends to be slow and stochastic. In natural and semi-natural ecosystem development, species invade slowly and can take advantage of the developing environment produced by physical and chemical changes that occur during succession. They can also take advantage, so to speak, of years when conditions for colonization are especially favorable. The establishment of species also depends on the source of propagules available in the vicinity. Since most grassland species have a limited dispersal capacity (Fenner, 1985; Van Dorp, 1996), the distances between seed sources and a target site are assumed to be of crucial importance. Ecological corridors could facilitate the dispersal of species under the assumption that they satisfy the requirements of desirable species in the target site (Verkaar, 1990). Although the application of island biogeography principles at several scales (i.e. national, regional and local) seems warranted for several medium to large vertebrate species (particularly birds and mammals), their applicability to plant species is not clear (Opdam *et al.*, 1993). Bakker (1989) identified two factors limiting the (re-)establishment of species. The first is the poor dispersal mechanism of many species and the second is the lack of gaps or safe sites (Harper, 1977; Green, 1983). In general, species with large seeds can grow through the established surrounding vegetation, but small-seeded species need gaps for their establishment. The occurrence of gaps is strongly determined by the management practices i.e. the timing and frequency of hay-making or the intensity of grazing.

Seed dispersal by hay-making machinery

In general, the dispersal of diaspores of most species does not cover large distances (Harper, 1977; Ter Borg, 1979). Most of the seeds land near the parent plants. Verkaar *et al.* (1983) showed that the dispersal of diaspores of chalk grassland species barely exceeds 2 m. Whereas 90% of the seeds in untouched plants of *Rhinanthus angustifolius* are dispersed within a radius of less than 25 cm, mowing during seed ripening results in a dispersal of over 2 m whereas the hay-making process sometimes adds another 6 to 7 m (Ter Borg, 1985). Obviously, hay-making machinery plays a role in the dispersal of species. Bakker *et al.* (1995) also focused on seed dispersal by hay-making machinery. They found that the machinery contained 1000-1500 seeds per gram of adhering material. On the basis of this they estimated that transport by hay-making machinery could account for over 1.000.000 seeds. Sampling seeds from the skid disk before the machinery entered the field and after cutting that field showed that seeds from species dominant in the vegetation were actually exported. Seeds from species absent in the established vegetation were actually imported. Given that the abundance in the vegetation and the numbers of seeds on the machinery showed a significant positive correlation, it can be inferred that in general no selection takes place by the machinery and most species are dispersed proportionally to their abundance, both within and between fields. However, some species were hardly found at all on the machinery, despite their abundance in the vegetation. This discrepancy may be attributed to their deviating period of seed set. However, it is clear that the process of hay-making can contribute to the dispersal of seeds by machinery which moves from one hayfield to another. Whether the dispersed species establish or not depends, among other factors, on the density of the sward.

Seed dispersal by grazing livestock and geese
Bülow-Olsen (1980b) and Hilligers (1985) suggested putting large herbivores on species-rich grasslands and then on areas under restoration management in order to facilitate the dispersal of seeds of species with nature conservation interest. They both believed that livestock play a role in the dispersal of species. Hillegers (1985) found seeds of the genera *Agrimonia, Carduus, Cirsium, Galium, Lappa* and *Cynoglossum* attached to the long fleece of Mergelland-sheep in the Netherlands. Bülow-Olsen (1980b) conjectured that *Pimpinella saxifraga, Campanula rotundifolia, Galium verum, Festuca ovina* and *Agrostis capillaris* had established in a grazed former heathland overgrown with *Deschampsia flexuosa* in Denmark after the cattle had grazed in a species-rich grassland which contained those species. In a study of seed dispersal in a sheep-grazed mixed grassland Bakker (1989) concluded that viable seeds of several species which occurred in the grassland area had been transported to the heathland area via dung pellets and/or wool fragments. Only the seeds of *Calluna vulgaris* were transported from the heathland area into the grassland area. In several other studies viable seeds were found in dung of grazing cattle (e.g. Müller, 1955; Boeker, 1959). Geese pellets may also account for the spread of some plant species (De Vries, 1961; Bakker, 1989).

Reintroduction of species
In many nature reserves and semi-natural areas one is trying to ameliorate the conditions of the habitats to stimulate the reappearance of lost species. One measure is to apply optimal management aiming at impoverishing of the soil. But if the desired species are not able to bridge the distance to the improved area or if this overbridging takes too long, this improvement of the biotope by optimal management will not lead to positive effects. Given the expense of ineffective management practices, this raises the question of whether it should be allowed or is even necessary to bring back the desired species by active reintroduction after ameliorating the conditions of the habitat. In artificial restoration of species diversity the required species are introduced artificially and sown by ordinary agricultural techniques. The choice of species can be tailored to suit the ecosystem being reconstructed, including species suitable for early as well as late stages of ecosytem development. An important consideration here is the provision of micro-environments for establishment which are suitable, both chemically and physically, for the desired species.

There are four methods of active reintroduction of species: 1) sowing, 2) strewing fresh mowings, 3) planting out seedlings or even adults, and 4) transplanting parts of vegetations. Reintroduction of individual species can be applied by sowing them or by planting them out. Sowing is preferred because planting out is in essence less natural than sowing (Van Groenendael *et al.*, 1998). By planting out the germinating phase and the susceptible juvenile stage are avoided. This prevents the environment from selecting and therefore the natural succession can be disturbed. When reintroducing plant species by sowing, the seeds used should preferably come from proximate populations (i.e. original ecotype). Strewing fresh mowings can be applied when the simultaneous reintroduction of several plant species or even a whole community consisting of grass and herb species is desired. A disadvantage of this method is that at any given time only part of the species have produced seeds that are able to germinate. This disadvantage can be overcome by mowing and strewing the fresh mowings at different moments through the summer season. Complete sods can be transplanted when the conservation of complete parts of vegetations including the topsoil is desired, especially when one or more rare species are involved. Sometimes the complete sods are used not only because of the vegetation present but also because of the seed bank included. It can be risky to use the original topsoil because a great deal of the seeds in it are of ruderal species. Even topsoil from well developed species-rich hayfields often contains more seeds of ruderal species than of the desired perennial species of stable grasslands (Wells, 1983).

Sowing and strewing fresh mowings are preferred as methods for reintroduction of plant species. Their advantage is that only the restrictions to the dispersion capacity are removed, whereas the other natural processes like germination and settling can take their normal spontaneous course. Besides, the soil is not disturbed.

National Ecological Network

In the Netherlands, the loss of biodiversity has been especially dramatic during this century. The greatest deterioration is in relatively nutritient-poor ecosystems (Bink *et al.*, 1994). The number of species on the Red List of plants that have already disappeared or are in danger of disappearing in the Netherlands is growing fast (Weeda *et al.*, 1990). Between 1970 and 1990, 55 of the 1449 species of

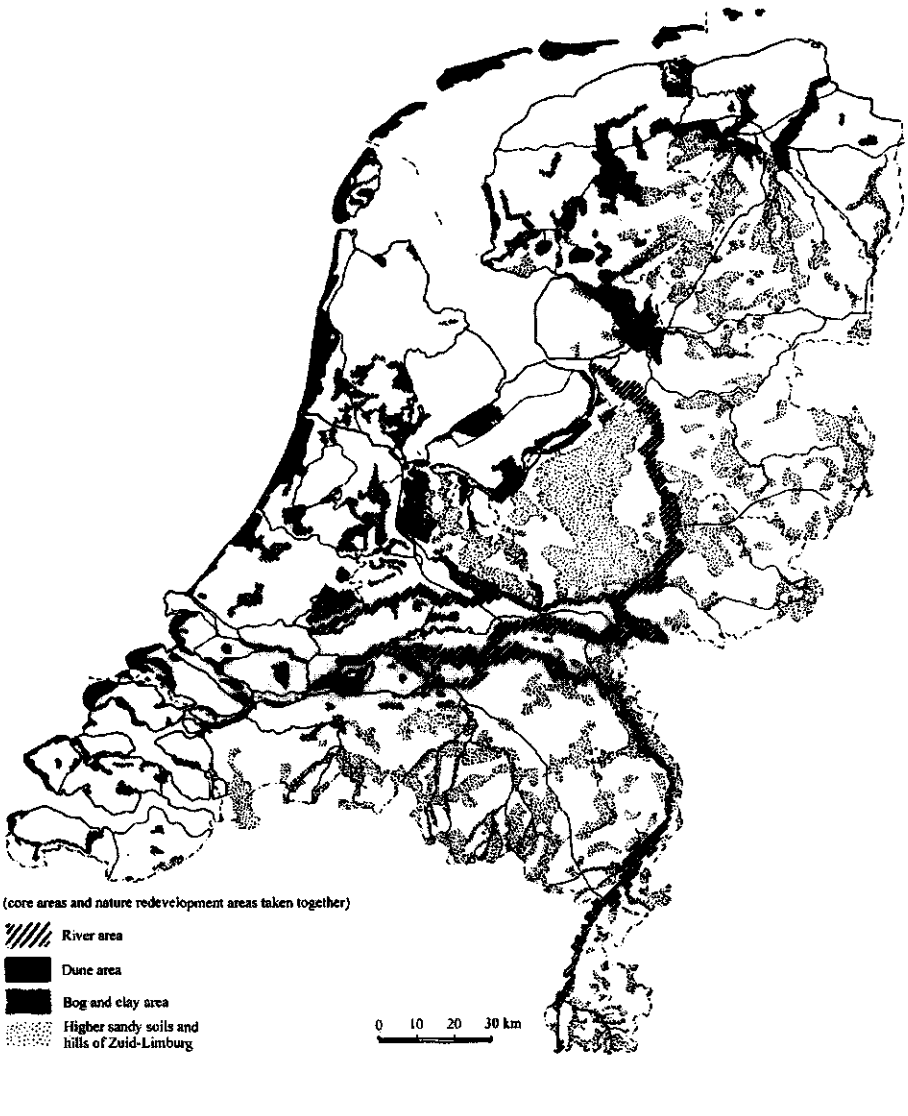

Figure 1. The National Ecological Network of the Netherlands (Source: Ministry LNV, 1990).

flowering plants recorded in the Netherlands disappeared and a further 486 declined seriously (Weeda *et al.*, 1990). In 1990 541 (i.e. 37.3%) of all native plant species had disappeared, or were endangered or potentially endangered. The Dutch List has considerably more endangered species than the Red Data Lists of the neighbouring German 'Bundesländer' Niedersachsen and Nordrhein-Westfalen. The factors responsible for this decline include the eutrophication and acidification of ecosystems, the falling water tables and the fragmentation of natural and semi-natural habitats (Van Dorp, 1996).

It has become increasingly apparent that it is important to have a wide-ranging policy on the conservation of nature, water (quality and quantity) and environment, which ensures the coherence and interdependence of these three aspects. Therefore, in the Netherlands, conservation policy has evolved to become an important part of a total policy on the environment and land use. The government's policy on nature conservation and landscape is important for the sustainable conservation, restoration and redevelopment of ecological features. In the late 1980s, the Dutch parliament endorsed several policy plans which aim to counteract the deterioration of nature. One of these, the *Nature Policy Plan* (Ministry LNV, 1990) specifically tries to preserve national biodiversity by developing a *National Ecological Network* or NEN. Essentially the National Ecological Network comprises a coherent network of existing and future conservation areas and is built up out of core areas, nature redevelopment areas (i.e. designated for habitat creation) and connecting zones (see figure 1).

The core areas consist of nature reserves, country estates, woodland, large surface water features and agricultural landscapes deemed to be of cultural and scenic merit. They must have special ecological value nationally and/or internationally. They function as the 'source' of the dispersal of plant and animal species over a larger area. Nature redevelopment areas are areas of good potential for developing ecological features. Initially the emphasis is on buying such terrains and landscaping them appropriately by excavating and enhancing the relief, or restoring the natural dynamics, so that a favourable starting situation can be created in which varied plant and animal communities will develop spontaneously. The National Ecological Network is supported by designating buffer areas around vulnerable areas, in which protective regulations are applied (e.g. on the pollution of the groundwater with fertilizers, and the influences of traffic and agriculture). Finally, the connecting zones interconnect the core areas and link them with the nature redevelopment areas, thereby enabling species exchange to take place and reducing the probability that species in formerly isolated areas will die out. Connecting zones therefore aim to counteract the many barriers such as roads, canals, built-up areas and intensively farmed areas that prevent many species from spreading from one habitat to another.

The ecological motive underlying the National Ecological Network is based on the island biogeographical principles of area-dependent extinction and area- and distance-dependent immigration (MacArthur & Wilson, 1967). According to this theory and later derivatives (Gilpin & Hanski, 1991), enlarging existing favourable areas through nature development will lead to larger populations and hence lower rates of extinction (Verboom *et al.*, 1993). Increasing the connectivity between isolated areas and decreasing the resistance to dispersing propagules and juveniles increases the numbers of immigrants and therefore the rates of (re)colonization. The applicability of island biogeography principles at several scales (i.e. national, regional and local) seems warranted for several medium to large vertebrate species (particularly birds and mammals), but their applicability to plant species is not clear (Opdam *et al.*, 1993).

1.2.3 Sustainability of species-rich plant communities

Semi-natural landscapes such as meadows, dune grasslands, reed swamps and heaths, they are man-made natural ecosystems, their presence being the result of a very regular, continued management (Sýkora & Sýkora-Hendriks, 1977). This human activity in most cases meant a periodic removal of the vegetation by mowing, burning, cutting sods or grazing, and it has gone on for centuries, sometimes even for many centuries, in the same way. These, by modern standards primitive, agricultural activities, which were limited to relatively small areas and which varied from place to place, enabled a great diversity, a relatively fine-structured vegetation pattern and a large number of species-rich communities to develop. Nowadays, however, agricultural activity has lost its enriching character by working upon the principle that the activity should be the same everywhere but that the treatment should change continuously from time to time. This has been enabled by the amplification and mechanisation of the agricultural activities. This has resulted in the floristic richness in the Netherlands dwindling drastically in the last 70 years, with most losses in the semi-natural vegetations (Westhoff, 1956, 1976; Van der Maarel, 1971, Van der Meijden *et al.*, 1990). Instead of the above-mentioned principle, spatial diversity should be maintained by varied but locally constant treatments of the land (Westhoff, 1970, 1971; Van der Maarel, 1975). Because of the great importance of semi-natural elements in the landscape, the remnants of the old semi-natural vegetation types should be preserved against further destruction by a responsible environmental management and, additionally, the area of semi-natural vegetation types should be enlarged by appropriate restoration management.

However, since island biogeography theory (MacArthur & Wilson, 1967) and models of metapopulation dynamics (e.g. Gilpin & Hanski, 1991) suggest that the species richness of a habitat is maintained by a dynamic equilibrium between both local extinction and local colonization (Tilman, 1993), furthermore, it is likely that attempts to recreate species-rich plant communities, by optimizing the management, will be most successful in a diverse landscape which can provide propagules of species in a large measure (Smith & Rushton, 1994).

1.3 THE VEGETATION ON RIVER DIKES

Nature conservation interest

The large variation in ecological factors caused by increased spatial variation is responsible for the high species diversity of semi-natural vegetations on Dutch river dikes. The various aspects and inclinations of the dike slopes, the various soil types they are made of, and the material used for paving the top of the dike are all of ecological importance for the vegetation (Sýkora & Liebrand, 1987; Sýkora *et al.*, 1990; Van der Zee, 1992). From the top to the foot of a dike there is a gradient from dry to moist. At the same time the soil at the foot is often more nutrient-rich than the relatively nutrient-poor soil on the top, as a result of the direct and indirect agricultural influence at the foot of the dike and the eutrophication of the river water during high water periods and of the water in the adjacent ditches. Both situations are favourable for species diversity (Van Leeuwen, 1966, 1967, 1968). Additionally, various parts of the dikes are treated in different ways, which also gives rise to great differences in species composition and diversity.

The decline of the floristic composition of the dike vegetation parallels developments in most other biotopes in the Netherlands. Between 1968 and 1992 as much as 89% of the locations with a dry floodplain grassland vegetation in the Netherlands disappeared (Van der Zee, 1992). At present the vegetation of more than 90% of the river dikes is species-poor grassland on which sheep graze, and rough vegetation mown for hay. Only about 7% of the surface area of the river dikes is covered by species-rich grasslands of the phytosociological syntaxa *Arrhenatheretum elatioris* and *Lolio-Cynosuretum*, both belonging to the *Arrhenatherion elatioris*. Only 1% is covered by the typical species-rich dry grassland *Medicagini-Avenetum*. At present the last remnants of these grasslands are in danger of disappearing. The deterioration in the semi-natural vegetation has mainly been caused by the fact that the slopes of the dikes are increasingly being used for agriculture (fertilization, overgrazing, use of herbicides) but also because ecological features were insufficiently taken into account while reinforcing the dikes. The decline of the floristic composition of the dike vegetation parallels developments in most other biotopes in the Netherlands. The greatest deterioration is occurring in relatively nutritient-poor ecosystems (Bink *et al.*, 1994). The number of species on the Red List of plants that have already disappeared or are in danger of disappearing in the Netherlands is growing fast (Weeda *et al.*, 1990).

Like road verges, river dikes have a very small area-perimeter ratio. The adjacent arable land mainly indirectly affects the vegetation through the use of artificial fertilizers, and the application of herbicides considerably reduces the number of species (Sýkora & Sýkora-Hendriks, 1977). Despite of this, in the contemporary Dutch agricultural landscape ribbon-like dikes and other ribbon-like biotopes like road verges can be of considerable ecological value. When managed in a proper way river dikes bearing species-rich vegetations with many rare species could function as a corridor between nature reserves and other areas important for the conservation of nature in the Netherlands. Insects in particular, but also small mammals and birds and probably also plant species take advantage of these longitudinal semi-natural elements in the landscape. According to Beeftink (1975) the dikes are important as plant migration routes between the 'river dunes' and terraces in the inland river valleys and the elevated sites of salt-marshes, dunes and rocky coasts on the seaside. Additionally, the small area-perimeter ratio enables river dikes to influence a relatively large bordering area. The ecological importance of river dikes justifies the effort and need for proper management and protection of species-rich dike grasslands.

The role of river dikes

The long snaking form of river dikes makes them ideal zones for connecting core areas and nature redevelopment areas, both areas that contain (or will contain) dry ecosystems and areas that contain wet ecosystems. Table 1 shows the total length of the river dikes in the Netherlands and their distribution over the various rivers.

Table 1. Total length of the Dutch river dikes and the proportions of the separate rivers (Source: Ministry LNV, 1986).

Rhine and Lek	184 km
Waal and Upper-Rhine	249 km
IJssel	227 km
Overijsselse Vecht	60 km
Meuse	282 km
Total length	1002 km

Until about 30 years ago, dry floodplain grassland vegetation was widespread on Dutch river dikes, and therefore it is believed that these dikes have good potential for the restoration of these species-rich grasslands, especially on south-facing inner slopes (i.e. land-facing). Although for safety reasons these inner slopes must meet requirements relating to stability and resistance to erosion, these are less stringent than those stipulated for the outer slopes. At high water levels the outer slopes have to resist strong water forces. The inner slopes only have to resist weak erosion forces if some water flows over the dike at extremely high water levels.

On some dikes, particularly those maintained by nature conservation agencies (e.g. National Forest Service), there are still well developed dry floodplain grassland vegetations, although these are rare. However, these are at great risk from the intensified agricultural activities on dike slopes and from the often large-scale civil engineering work being done to reinforce the dikes. These surviving valuable dry floodplain grassland vegetations must be cherished and, whenever possible, spared during the dike improvements.

Geobotany

In 1929 Van Soest was the first to distinguish a number of geobotanical districts on the basis of species with a common distribution pattern within the Netherlands. A more complete picture of the distribution patterns of the native species has since given rise to a change in this classification (Weeda, 1988, 1989). The Delta district has been separated from the Fluviatile district and is now called the Estuarine district (see figure 2). The term 'geobotanical district' has been replaced by 'floral district'.

The Fluviatile district is one of the best characterized floral districts in the Netherlands (Weeda, 1990). Dozens of species are either related or restricted to this district and to only one or a few other districts. These species are also called *floodplain plants* (Sloff & Van Soest, 1938, 1939). In most cases they have spread along the rivers from Central Europe to the low countries (Tüxen, 1950). On the slopes of the river dikes only dry floodplain plants occur, whereas others prefer wet habitats. Dry floodplain plants mainly occur in dry grasslands but also in woodland margins, both on calcareous soil (Neijenhuijs, 1969). In the Fluviatile district they mainly grow on natural sandy river embankments and on artificial dikes.

D: Drents district
E: Estuarine district
F: Fluviatile district
G: Gelders district
H: Haf districts (E, L, N)
K: Kempens ditrict
L: Bog district
N: Northern clay district
P: Pleistocene districts (D, G, K, S, V)
R: Reno-dunal district
S: Sub Central European district
V: Flemish district
W: Wadden district
Y: IJsselmeer polders
Z: Zuidlimburgs district

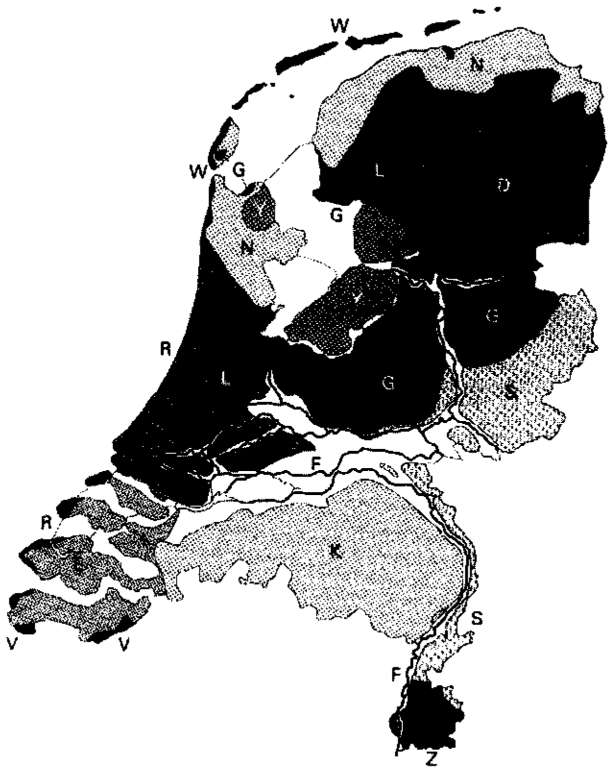

Figure 2. Floral districts in the Netherlands (Source: Weeda, 1989).

As the Rhine basin is the main migration route of the floodplain plants, the Rhine region in the Fluviatile district contains the most species-rich flora. This area comprises the valleys of the Oude IJssel, Gelderse IJssel, Rhine, Kromme Rhine, Lek, Waal and the confluence of the Meuse and Waal. The Meuse area has hardly any species that are unique to the area; part of the floodplain flora probably found its way from the Rhine area into the Meuse valley (Drok, 1988).

Plant communities
For civil engineering reasons the ground cover allowed on river dikes usually consists of grassland. Some scrub may be allowed to grow here and there on the inner slopes and some parts of the outer slopes of the dikes. Trees are not allowed, because their roots may put the stability of the body of the dike at risk. The potential natural vegetation, which is woodland in most parts of the Netherlands, does not occur on river dikes. The grassland vegetation on the dikes exists solely because of human activities such as mowing, burning and livestock grazing. At present more than 90% of the grassland vegetation found on dikes in the Netherlands is exploited by farmers, for livestock (mainly sheep) production (Van der Zee, 1992). The varieties of grass species sown here are specially bred for persistence, and the grass is used for making hay and grazing. About 65% of the grassland is used for grazing sheep and has very few plant species, and 25% is rough and highly productive hay land.

Unlike this 'production grassland' the *floodplain grassland vegetation* is semi-natural. It consists mainly of native plant species, but its structure and appearance have been strongly influenced by man. The composition of the *floodplain grassland vegetation* corresponds with that of the natural vegetation on alluvial ridges and naturally higher ground along the rivers. *Floodplain grassland vegetation* on dikes can only exist with the human help. The *floodplain grassland vegetation* is able to develop on river dikes because of the specific soil properties and the physical circumstances (slope, aspect) of the dike slopes. Appropriate management, with very little use of fertilizer, is also important.

The question now is what conditions should be created to enable a similar vegetation to return after the necessary reinforcement of the river dikes. If the valuable, species-rich *dry floodplain grassland vegetation* is to return, the habitat before and after the reinforcement of the dikes must be the same. Replacing the original sods or sod soil after the reinforcement provides a topsoil of similar composition to that before the reinforcement. Usually the angle of inclination of the dike berm changes with the reinforcement. This may have implications for the composition of the vegetation. Steeper slopes, especially those facing south, dry out more in summer than those that are less steep. That is why they are favoured by dry-grassland species. The original habitat of this thermophilous flora is on natural sandy river embankments and alluvial ridges in the floodplains. For all sorts of reasons the original growing sites have deteriorated rapidly in the last 30 years, and certain plant species have therefore become increasingly scarce and are in danger of disappearing from the Netherlands (Weeda *et al.*, 1990).

In general, Dutch river dikes are covered with anthropogenic grasslands and tall forb communities (Westhoff & Den Held, 1969) of the class of moist to relatively dry, neutral grasslands, the *Molinio-Arrhenatheretea*. For the full names of the syntaxa, see figure 3. In 1996 Schaminée *et al.* published a revision of the *Molinio-Arrhenatheretea*. In this thesis the classification of Westhoff and Den Held (1969) is followed. In § 3.4.1an adjustment to the review of Schaminée *et al.* (1996, 1998) is presented. According to Westhoff and Den Held (1969), within the *Molinio-Arrhenatheretea* the moist and dry hay meadows and pastures are assigned to the *Arrhenatheratalia*, which has only one alliance in the Netherlands, the *Arrhenatherion elatioris*. The *Arrhenatherion* consists of a (possibly fertilized) grassland vegetation on moist, fertile soils, especially on loam, clay and sandy-clay soils. They are grazed regularly or are mown at least twice a year. The herbaceous layer has a relatively high percentage of Leguminosae. On river dikes there are two associations: *Arrhenatheretum elatioris* and *Lolio-Cynosuretum*. The *Arrhenatheretum elatioris* is a hayland community which is only occasionally grazed before and/or after mowing. In the Netherlands grazing occurs more often than in other European countries, where this vegetation is rarely grazed. This community is found on very fertile, not necessarily fertilized clay and sandy-clay soils with a varying moisture content. It is a substitute community for the *Alno-Padion*. Two sub-association groups occur on dikes. Group A consists of two sub-associations: *alopecuretosum*, which grows on moist soil, especially in endiked floodplain areas, but also on dikes (mainly at the foot), and sub-association *inops*, which occurs in less moist places, both in the endiked floodplain and on the dikes. Sub-association group B also comprises two sub-associations: *picridetosum* is a sub-ruderal community, occurring mainly on relatively dry and fertile soil, and sub-association *brizetosum* is found on relatively dry, less fertile soil. The *Lolio-Cynosuretum* is a grazed pasture. Often however, grazing is combined with haymaking and the grassland is grazed before and/or after mowing. This community is maintained by continuous, rather intensive grazing, trampling and manuring. It is restricted to regions with a mild climate in which grazing can take place for most of the year. This community can be found on many soil types. Two sub-associations occur on and along dikes, and on sandy ridges in the endiked floodplain: *ononidetosum* and *plantaginetosum mediae*. These sub-associations form a transition to the *Medicagini - Avenetum pubescentis*.

In the drier, sandier places on river dikes, especially on south-facing slopes, species of the drier grasslands occur. These belong mainly to the class of dry calcareous grasslands *Festuco-Brometea* and to a lesser degree, the class of sandy, dry grasslands *Koelerio-Corynephoretea*. These species are in danger of disappearing from the Netherlands (Bink *et al.*, 1994; Weeda *et al.*, 1990; Westhoff *et al.*, 1970).

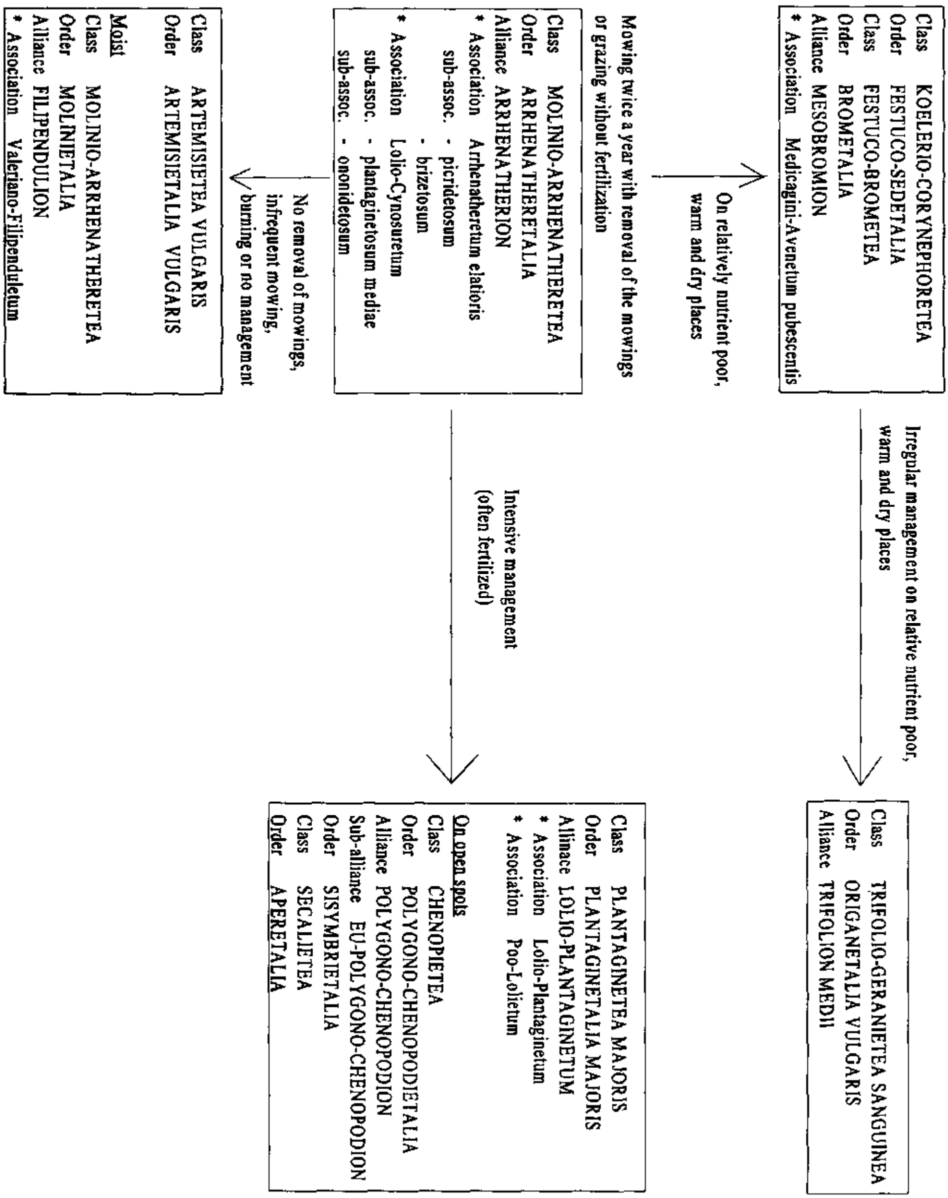

Figure 3. Main plant communities on river dikes and relation with management and habitat conditions.

Species characteristic of the *Trifolio (medii)-Agrimonietum* are found in sunny places on the slopes of dikes managed less regularly. In the revision of Schaminée *et al.* (1996) this community is called *Rubo-Origanetum*. This association belongs to the *Trifolion-medii*, the only native alliance of the *Origanetalia vulgaris*. In the sites concerned, the association is a substitute community for woodlands and shrubby vegetations. In sites experiencing some disturbance (e.g. from much trampling and/or grazing), species of the *Plantaginetea majoris* grow. The communities of this class are largely made up of perennials, mainly rosette hemicryptophytes and creeping hemicryptophytes, with runners. The disturbed environments are unstable and transitory, although their instability is never so great that the vegetation is periodically destroyed or almost destroyed, allowing therophytes to dominate.

Species of the *Artemisietea vulgaris* are found in sites where mowing is insufficient or where the mowings are not removed. This class consists of natural and anthropogenic communities with tall perennial herbs, mostly hemicryptophytes and partly geophytes and climbers. Ruderal communities consisting predominantly of annual and biennial species are classed as *Chenopodietea*. These communities, to which the weed communities of the root-crop fields also belong, mostly occur in places where the soil has recently been ploughed or dug and is temporarily bare. In these situations many species of the class of *Secalietea* appear. These communities also consist largely of annual and biennial species. The grasslands that are grazed and fertilized most intensively have very few species, and belong to the *Poo-Lolietum*. This community occurs over very large areas in the Netherlands and is still increasing. In figure 3 the links between the plant communities mentioned above and management is shown schematically.

1.4 THE RECONSTRUCTION AND IMPROVEMENT OF DUTCH RIVER DIKES

High water-levels occurred several times in the first half of this century, giving rise to critical conditions in the lower-lying parts of the Netherlands. The disastrous flood of 1953, in which 2000 people perished, led to the decision in 1956 to reconstruct the main dikes along the large rivers, to withstand a maximum flow rate of 18,000 $m^3.s^{-1}$ of the Rhine near Lobith (the probability of occurrence is once in 3000 years). This decision was formalized in the Delta Act. However, resistance to the plans for dike reinforcement began to grow once the implications for the cultural history and natural history in the scenic river area became evident. This led to the Committee for River Dikes (Commissie Becht) being set up in 1975 by the then Minister of Transport and Public Works to examine the proposed measures for dike reinforcement. In its final report the committee recommended reducing the normative high water (MHW; maatgevend hoogwater) of the Rhine at Lobith to 16,500 $m^3.s^{-1}$. This has a probability of occurrence (and therefore of flooding) of once in 1250 years. The committee also advised sparing the scenic value as much as possible by applying 'optimized designs'. In a publication issued by the 'Construction and Management of Grass Cover on River Dikes' working group of the Advisory Technical Committee for Dams, the high botanical value of river dike grassland vegetations was stressed (Technische Adviescommissie voor de Waterkeringen, 1981), and the measures to be taken during construction and management to maintain or possibly increase the quality of the vegetation were discussed.

However the scenic, cultural, historical and ecological features of the river area continued to deteriorate because the recommendations of the Becht Committee were only partly followed. This decline was accompanied by an increase in public criticism of the impact of dike reinforcements on the scenery along the rivers. On the one hand, doubts grew about whether the safety standards were too stringent and on the other hand the conservation of the remaining scenic, natural and cultural features was stressed. In addition, ideas about the intrinsic value of the river area changed. Nowadays this value is no longer expressed in terms of the number of elements such as houses, on or next to the dike, pools and trees. The river dikes have become more important in the perception of the scenery as a whole and their cultural, historical, social and ecological value are becoming appreciated more and more. Now, river dike improvements threaten to dramatically reduce this value.

In 1992 the Committee for Testing the Principles of River Dike Reinforcement was established (Committee Boertien I). In its final report (Ministry LNV, 1993) this committee proposed improving existing procedures by integrating several new elements. At strategic level they advocated making a provincial policy plan for dike reinforcements, specifying the starting points for dike reinforcements. The plans at project level would to be tested against these starting points and would also be subjected to an environmental impact assessment (the latter serves as an external check of the reinforcement plans). The committee also concluded that it was important that all the authorities concerned approach the implementation of the desired protection against flooding creatively, so that the existing ecological features of the river area would be spared as much as possible.

In December 1993 the Meuse attained high water levels comparable with those attained in the 'disaster year' of 1926. The Minister of Transport and Public Works therefore set up yet another committee: the 'Meuse Flood Disaster Committee', also known as 'Boertien II', with the remit to draw up an advisory plan containing a set of measures to reduce the high-water problems in the Meuse area where there were no main dikes. The final recommendations contained in 'Bring back the Meuse' were that in order to achieve protection against floods with a one in 250 years probability of occurrence, the summer bed should be widened and deepened and the winter bed dug out, and that small dikes should be constructed throughout the Meuse area where there were no primary dikes.

In January 1995 the water was extremely high again, and again a great part of the Meuse valley was inundated. This time the water level in the Rhine was so alarmingly high that it was decided to evacuate roughly 250 000 inhabitants from the vicinity of the river area. The 1995 flood alert accelerated various matters (*Anon.*, 1995):

a) it was agreed that the most critical sections of the dikes would be reinforced before the end of 1996,
b) the remaining sections would be reinforced before the year 2000,
c) the construction of the small dikes along the Meuse proposed by the Meuse Flood Disaster Committee would be speeded up,
d) a 'Large Rivers Delta Plan' would be prepared, suggesting that procedures for reinforcing the dikes be optimized and accelerated, and advising that the plans of the 'Testing the Principles of River Dike Reinforcement' and the 'Meuse Flood Disaster' committees be taken into account. A distinction would probably be made between the procedures for 1995 and 1996 and those for the period thereafter. The recommendations made by the Boertien I committee were to be noted especially when fleshing out the procedures for 1995 and 1996. It was thought that, if the design could be agreed on after sufficient dialogue with those concerned, was specifically aimed at reducing damage to scenery, nature and cultural features, and was used wherever and whenever possible, it could be implemented faster and, concomitantly, with widespread support.

1.5 Experimental research

In those instances in which it is impossible to spare the landscape, ecological and cultural features the question arises of whether these features can be reinstated after dike reinforcement, and how. In the research project described in this thesis the core questions were whether the valuable, species-rich vegetation on the dikes can return after reinforcement works and, if so, what are the pre-conditions for this during and after the reinforcement. Clearly, appropriate measures are necessary in order to give the dry floodplain grassland vegetation some chance to survive on the dikes. Therefore, the Directorate General for Public Works and Water Management commissioned Wageningen Agricultural University to start a research project to ascertain the optimum structure and growing conditions for the grass cover on river dikes. The conclusions drawn from this research project were that a species-rich dry floodplain grassland vegetation can only exist if certain conditions are met, not only with regard to habitat, but also with regard to management (Sýkora & Liebrand, 1987). A dry floodplain grassland vegetation only exists on relatively light substrate (maximally 25% clay) and strongly prefers south-facing calcareous slopes. The steeper the slope, the greater the probability that rare species will grow there. The research area was in the east of the Netherlands. In 1988 this project was continued on the dikes along the Meuse and further west in the Netherlands. The data of both regions were combined and synthesized (Van der Zee, 1992). The next step was to test the practical feasibility of the ecological engineering measures proposed in the above-mentioned projects. It was for this reason that an investigation was started in 1987 into the effects of ecological engineering measures during and after dike reinforcement. This investigation was based on the following working hypothesis:

It is possible to restore the extensive, valuable, species-rich grasslands that used to exist on the slopes of the Dutch river dikes by means of ecological engineering measures during dike reconstruction, followed by appropriate management.

This research project attempts to answer the following four questions, the first is more fundamental, the last three are very practical and especially concerning river dikes:

1. What is the relationship between the aboveground biomass, the structure of the vegetation, the soil fertility and the abundance of species?
2. Is it possible to speed up the reappearance of species-rich dry floodplain grassland vegetation by replacing the original topsoil as the new toplayer after the reconstruction?
3. What is the effect of different seed mixtures?
4. Given the different ways of re-establishing the dry floodplain grassland flora, which management strategy will lead to a favourable result in terms of ecological and civil engineering (i.e. high conservation value, great capacity to prevent erosion thanks to good ground cover and well-developed roots)?

CHAPTER 2

RESEARCH SITE AND EXPERIMENTAL SET-UP

2.1 LOCATION OF THE EXPERIMENTAL RIVER DIKE

In 1985 the experiment started on a dike along the river Waal, located east of Zaltbommel (51°49'N, 5°17'E), in the province of Gelderland in the south of the Netherlands (see figure 6). The experimental part of the dike is approximately 3.5 km long. It is supervised by the Polder Administration (Polderdistrict Groot Maas en Waal).

The experimental part of the dike was reconstructed between 1985 and 1987, in accordance with the standards laid down in the 1956 Delta Act. In order to save the oxbow-lake which lies in a nature reserve just outside the river dike, an 'optimized design' was applied when reconstructing the experimental dike. The outer-facing (i.e. river-facing) slope therefore deviated from the prescribed statutory specifications: it was reinforced with basalton (polygonal concrete blocks) and paving through which grass is permitted to grow (see figure 4). Additionally, in one place wooden piling was used to guarantee the stability of the dike.

The research was carried out on the landward slope of the experimental dike. Most of this slope faces south but a small part faces north-west (see figure 6). Slopes with a southerly aspect favour the development of species-rich grasslands. The gradient of the landward slope of reconstructed dikes is normally 1:3 (i.e. 30° or 33%). For this experiment the gradient of the lower landward slope was made to be 1:4 (i.e.) and that of the upper slope was 1:2 (see figure 4). On lower sections the gradient of the slope changed to 1:20 (stabilizing bank) and then to 1:5 (transition to the hinterland).

2.2 METHODS OF RECONSTRUCTION, SOWING AND MANAGEMENT

The experimental dike was divided into sections A to G (see figure 6). Each section was reinforced in a different way. Within a section there was a variation in gradient. The steeper part was sometimes reconstructed in a different way than the less steep part. For instance, the steep part (1:2) may consist of former topsoil, with the less steep part (1:4) consisting of imported clay. Each section contained a number of trial plots, each of

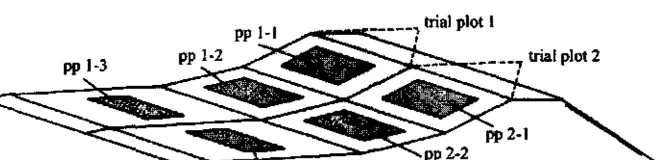

Figure 4. Cross-section of the experimental dike.

Figure 5. Schematic representation of part of the experimental dike, showing several trial plots and permanent plots (pps).

which was managed in a certain way. These plots varied in size. Their length varied: in general, pasture plots were longer than plots for hay making. The widths also differed. In most cases the trial plots contained a steep (1:2) and a less steep (1:4) part. Some also contained an almost level part (1:20) (see figure 4).

Permanent plots were sited in each part of the trial plot with a different method of reconstruction or a different gradient (see figure 5). Thus, a permanent plot consists of a part of the experimental dike that is reconstructed in a certain way, with a certain gradient and a certain management. The size of the permanent plots was 6 x 4 m, except in the section with the 'spared zone' (i.e. zone in which the original vegetation was spared: see 'Methods of reconstruction'). As the spared zone was only 2 to 3 m wide, the permanent plots were 12 x 2 m. The corners of the permanent plots were recorded in relation to the hectometre posts on the dike. In total there were 125 trial plots and 304 permanent plots. Table 2 shows the distribution of the trial plots and the permanent plots over the sections of the experimental dike.

Table 2. Distribution of the trial plots and permanent plots over the sections of the experimental dike.

Section	Trial plots	Permanent quadrats
Different ways of reconstruction	Different ways of management	Different ways of reconstruction, gradient and management
A	40	80
B	15	36
C	9	27
D1	7	14
D2	7	14
E1	4	8
E2	5	10
E3	4	8
F	8	16
G1	6	12
G2	16	63
G2'	4	16
Totals	125	304

Methods of reconstruction

The methods of reconstruction studied in this research were:

a. sparing part of the original slope with the original vegetation,
b. replacing the original 0-25 cm layer;
    b1 in the form of sods, carefully removed by hand and left intact,
    b2 as topsoil (i.e. the uppermost 25 cm of soil, containing propagules); this soil was disturbed and mixed by digging,
c. replacing the original 25-50 cm layer as the new top layer,
d. using imported clay, containing no propagules of the vegetation present on the dike before reconstruction, as the new topsoil.

Table 3 shows which methods of reconstruction were applied in the various sections and also the number of permanent plots per method of reconstruction. Section D was divided into two sub-sections on the basis of different aspect (see figure 6). The aspect of section D1 is mainly north-west and that of D2 is west. Section E was divided into three sub-sections, differing in method of reconstruction (see table 3). Section G2 was divided into two sub-sections. In G2' a bend in the dike was corrected and therefore no zone was spared.

Procedure during dike reconstruction

Propagules like rhizomes, tubers and bulbs and seeds of many species do not survive long when buried. Therefore the earth removed from the dike must not be stored too long before it is replaced. The experimental dike was reconstructed section by section, and the earth removed was stored for only two to four weeks before being replaced in situ. To ascertain whether watering benefits the recovery of the original vegetation, part of the dike was watered after the original topsoil had been replaced.

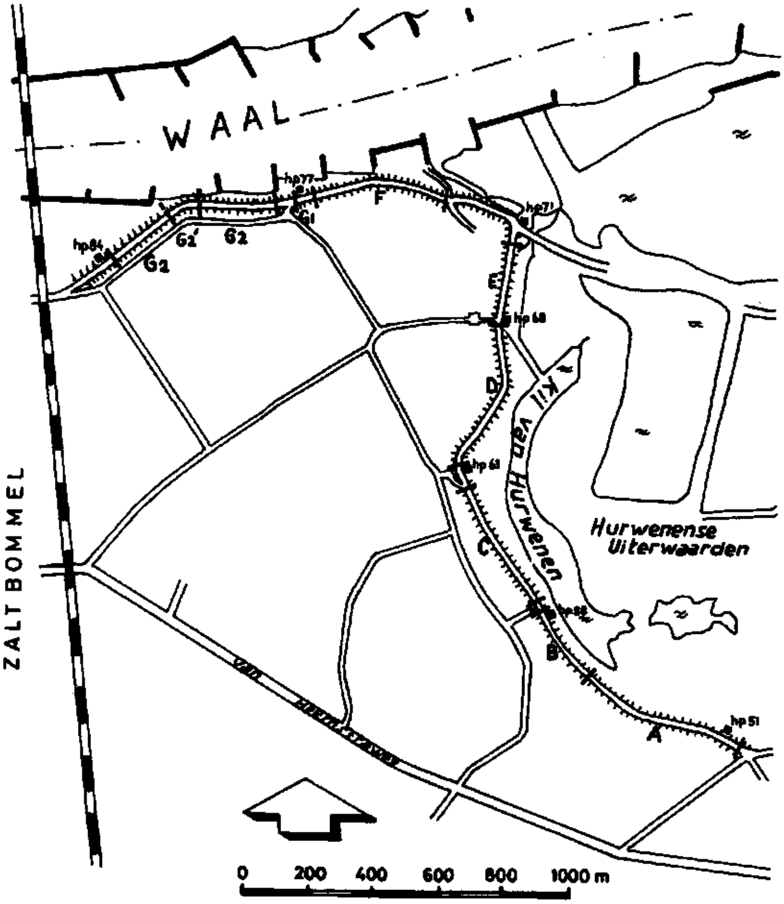

Figure 6. Location of the experimental dike. Sections A to G2 are indicated separately.

Sowing treatments

Five seed mixtures were used:

a. LGM: seeds of grasses and herbs collected on the experimental part of the dike before reconstruction,
b. D1: standard dike mixture,
c. BG5: standard mixture for pastures,
d. Lm: *Lolium multiflorum* (Italian rye-grass),
e. combinations of seed mixtures: D1+LGM, BG5+LGM, Lm+LGM,
f. no seed sown (control).

The various sowing treatments applied to the experimental dike are shown in table 4.

Tabel 3. Methods of reconstruction in the different sections and the number of permanent plots per method of reconstruction. On replaced former topsoil: a; topsoil replaced on original steep gradient (1:2), b; topsoil replaced on original less steep gradient (1:4), c; topsoil from less steep gradient (1:4), replaced on steep gradient (1:2), d; topsoil from steep gradient (1:2), replaced on less steep gradient (1:4).

Section	Spared zone	Replaced sods	Replaced topsoil a	b	c	d	Replaced subsoil	Imported clay	Total
A	.	.	.	.	.	40	40	.	80
B	.	.	.	.	.	15	15	6	36
C	.	.	.	.	9	9	.	9	27
D1	.	.	7	.	.	7	.	.	14
D2	.	.	7	.	.	7	.	.	14
E1	.	.	.	.	.	.	.	8	8
E2	.	.	5	5	.	.	.	.	10
E3	.	4	.	.	.	.	.	4	8
F	.	.	.	.	.	.	.	16	16
G1	.	.	.	.	.	.	.	12	12
G2	16	.	.	15	.	.	.	32	63
G2'	.	.	.	.	.	4	.	12	16
Total	16	4	19	20	9	82	55	99	304

Table 4. Number of permanent plots per section in which the different sowing treatments were applied.

Section	Not sown	LGM	D1	D1 + LGM	BG5	BG5 + LGM	Lolium mult.	Lolium mult.+ LGM	Total
A	38	14	.	.	.	.	14	14	80
B	.	.	.	.	29	7	.	.	36
C	.	.	9	18	.	.	.	.	27
D1	.	.	.	14	.	.	.	.	14
D2	.	.	.	14	.	.	.	.	14
E1	.	.	.	.	8	.	.	.	8
E2	.	.	.	10	.	.	.	.	10
E3	4	.	.	4	.	.	.	.	8
F	.	.	.	16	.	.	.	.	16
G1	.	.	.	12	.	.	.	.	12
G2	16	.	.	47	.	.	.	.	63
G2'	.	.	.	16	.	.	.	.	16
Total	58	14	9	151	37	7	14	14	304

The LGM mixture was collected by mowing and threshing in July 1986, a year before the dike reconstruction. Hardly any recent data were available on the dike flora before the reconstruction. However, the vegetation in the spared zone might indicate what the vegetation looked like before reconstruction. The only other information available consists of an inventory by a local nature organization in which the grass species were omitted (Natuurwacht Zaltbommel, 1978) and a few relevés made in 1984 and 1985 for a study on the civil engineering and ecological engineering aspects of river dike vegetation (Sýkora & Liebrand, 1987) and for an inventory made by the Province of Gelderland. These relevés represented the vegetation on only a few locations on the experimental dike before 1987. However, the fact that so few relevés were made before 1987 suggests that there was little variation in vegetation composition on the dike before the reconstruction. On the other hand, it can be expected that relevés tend to be made of the best developed vegetation, and therefore they will provide a good picture of the species which occurred before the reconstruction.

The management of the vegetation before the reconstruction was irregular (see § 3.2.5). Most parts of the dike had been mown twice a year, but parts difficult to reach - especially those on the lower parts of the dike - were often left unmown. The vegetation in these parts must have been very rough; this was confirmed by slides taken by Grontmij Consultancy just before the dike reconstruction. The mowings were only removed if the weather was favourable for hay-making, otherwise they were left in situ, as was done on almost all river dikes then. The slides taken by Grontmij Consultancy were snapshots of the vegetation at a certain moment, but from these it could be concluded that the former vegetation at the locations photographed was relatively productive and consisted of many tall, ruderal herbs such as *Heracleum sphondylium*, *Anthriscus sylvestris*, *Symphytum officinale*, *Calystegia convolvulus*, *Urtica dioica*, *Rumex obtusifolius*, *Rubus caesius* and *Cirsium arvense*. Species such as *Phragmites australis*, *Phalaris arundinacea*, *Valeriana officinalis* and *Filipendula ulmaria* also indicated ruderalization but also relatively damp conditions. *Arrhenatherum elatius*, *Dactylis glomerata*, *Alopecurus pratensis*, *Elymus repens* and *Phleum pratense* were probably the most frequent grass species. Plant species of greater botanical value could only be found sporadically, on intermittently well managed locations. Actually, the LGM seed mixture largely consisted of seeds of False oat-grass *Arrhenatherum elatius*, with small amounts of other grasses and herbs. In most of the sub-sections sown with only LGM, a standard D1 mixture was sown later at a low rate (see table 4).

The standard dike mixture D1 consists of Perennial rye-grass *Lolium perenne* pasture type (34%), Smooth meadow grass *Poa pratensis* (34%), Red fescue *Festuca rubra* with fine runners (34%), ditto with strong runners (8%) and cultivated White clover *Trifolium repens* (6%) (Anon., 1991). D1 is intended for dikes that will be grazed or used for a hay crop. It contains an appreciable proportion of Perennial rye-grass, a species which establishes rapidly and therefore quickly fixes the soil. Because it germinates much more rapidly than the other species, in practice *Lolium perenne* often becomes dominant immediately after sowing, even though it forms only 34% of the seed mixture. As well as being very tasty, White clover promotes productivity of the grassland vegetation, especially in the summer (Anon., 1991). The Red fescue and Smooth meadow grass are hardy and have creeping rhizomes. They form a strong, closed turf. Red fescue is less tasty. Given adequate moisture, good fertilization and regular grazing, Perennial rye-grass survives well. If conditions are dry and less fertile, Red fescue and, to a lesser extent, Smooth meadow grass, will dominate.

BG5 consists of Perennial rye-grass *Lolium perenne* pasture type diploid (33%), ditto late hay type diploid (23%), Meadow fescue *Festuca rubra* pasture type (7%), ditto hay type (7%), Timothy *Phleum pratense* pasture or intermediate type (7%), ditto hay type (7%), Smooth meadow grass *Poa pratensis* (3%), White clover *Trifolium repens* pasture type (3%) and cultivated White clover (10%) (Anon., 1991). Sowing a mixture of different grasses reduces the likelihood of disease and frost damage (Anon., 1991). White clover improves the taste of the crop and is present in very variable amounts in pastures. It increases under dominant mowing and in dry years. BG5 is suitable for sowing on normal moisture-retentive soils.

Italian rye-grass *Lolium multiflorum* is in general an annual species or at the most it can be short-lived (Weeda *et al.*, 1994). Italian rye-grass was sown to ensure the dike would go into the winter with a green sward. It grows until late in the autumn and then declines sharply in subsequent years, allowing the original vegetation to redevelop.

Combinations of the above mixtures (Lm+LGM and BG5+LGM) were sown in sub-sections A and B. A large part of sub-section A was left unsown, to allow the species present in the replaced soil or colonizing by natural dispersion from the surroundings, to establish without competition with species sown in the seed mixtures. In this way the original vegetation gets an optimal chance to redevelop without hindrance from sown species.

Management treatments

All management treatments applied on Dutch river dikes were also applied on the experimental dike.These are mowing, grazing, combinations of mowing and grazing and burning. The absence of management (no management) was used as a control. Variation in the intensity and timing was introduced into each of these treatments. As much as possible, the same management strategies were applied to all sections (see tables 5 and 6). The management treatments are described in detail below.

Table 5. Management treatments, expressed in number of trialplots in the sub-sections. 2xM = mown twice yearly, 1xMl = mown once yearly, late (in autumn), 1xMe = mown once yearly, early (in spring), 1xM/2y = mown every two years (in autumn), 2xG = grazed intensively twice yearly, M+G = mown in spring and grazed intensively in autumn, G+M = grazed intensively in spring and mown in autumn, Gseas = grazed extensively throughout the summer, + = mowings removed, - = mowings not removed, +/- = mowings removed in spring but left in autumn.

Management	2xM	2xM	2xM	1xMl	1xMe	1xM/2y	Burnt	No manag	2xG	M+G	G+M	Gseas	Total
Mowings	+	-	+/-	+	+	+				+	+		
A	8	6	2	6	2	4	.	.	4	4	4	.	40
B	2	2	.	2	1	2	.	.	.	2	2	2	15
C	1	1	.	1	.	1	.	1	1	1	1	1	9
D1	1	1	.	1	1	.	.	.	.	1	1	1	7
D2	1	1	1	1	1	1	1	.	.	.	.	.	7
E1	1	1	.	1	.	1	.	.	.	.	.	.	4
E2	1	1	.	1	.	1	.	.	1	.	.	.	5
E3	1	1	.	1	.	1	.	.	.	.	.	.	4
F	1	1	.	1	.	1	.	.	1	1	1	1	8
G1	1	1	.	1	1	1	.	.	1	.	.	.	6
G2	3	2	1	2	1	3	.	.	1	1	1	1	16
G2'	1	1	.	1	.	1	.	.	.	.	.	.	4
Total	22	19	4	19	7	17	1	1	9	10	10	6	125

Table 6. Management treatments, expressed in number of permanent quadrats in the various sections. Symbols explained in table 7 and figure 6.

Management	2xM	2xM	2xM	1xMl	1xMe	1xM/2y	Burnt	No manag	2xG	M+G	G+M	Gseas	Total
Mowings	+	-	+/-	+	+	+				+	+		
A	16	12	4	12	4	8	-	-	8	8	8	-	80
B	4	4	-	4	2	4	-	-	-	6	6	6	36
C	3	3	-	3	-	3	-	3	3	3	3	3	27
D1	2	2	-	2	2	-	-	-	-	2	2	2	14
D2	2	2	2	2	2	2	2	-	-	-	-	-	14
E1	2	2	-	2	-	2	-	-	-	-	-	-	8
E2	2	2	-	2	-	2	-	-	2	-	-	-	10
E3	2	2	-	2	-	2	-	-	-	-	-	-	8
F	2	2	-	2	-	2	-	-	2	2	2	2	16
G1	2	2	-	2	2	2	-	-	2	-	-	-	12
G2	12	8	4	8	4	12	-	-	4	4	4	3	63
G2'	4	4	-	4	-	4	-	-	-	-	-	-	16
Total	53	45	10	45	16	43	2	3	21	25	25	16	304

Mowing

Different kinds of mowing management were applied. In the case of hay-making the mowings were removed whereas in the case of mulching they were left in situ. The following combinations were applied: hay-making twice a year (in June and September), mulching twice a year (in same months), hay-making in June followed by mulching in September, hay-making once a year in June or in September and hay-making once every two years in September. In June, mowings are removed as hay, after drying for a week. In September, mowings are mostly removed immediately after mowing. Drying is not possible except for relatively warm September months.

Grazing

Table 7. Legend for tables 8, 9 and 10. Explanation of the codes.

Dike reconstruction	
SZ	spared zone
SOD	sods; complete sods removed and replaced manually
RTS	replaced topsoil; soil from 0-25 cm
	RTS a topsoil replaced in situ (steep: 1:2)
	RTS b ditto (less steep: 1:4)
	RTS c topsoil from less steep area (1:4); replaced on steeper slope (1:2)
	RTS d topsoil from steeper slope (1:2); replaced on gentler slope (1:4)
RSS	replaced subsoil; soil from 25-50 cm
IC	imported clay; sandy clay imported from elsewhere
Sowing	
1	not sown
2	LGM
3	D1
4	D1+LGM
5	BG5
6	BG5+LGM
7	Lm
8	Lm+LGM
Management	
2xM	mown twice yearly
1xM	mown once yearly
1xM/2y	mown once every two years
M+G	mown in spring, grazed in autumn
G+M	grazed in spring, mown in autumn
2xG	grazed twice yearly
Gseas	grazed extensively throughout summer
Br/Burning	burnt once yearly (late February/early March)
0/No manag	no management (left alone)
Removal of mowings	
+ / +r	mowings removed
+- / +-r	removed in spring, left in autumn
- / -r	mowings left in situ
Timing of mowing	
e / el	early; late May/early June
l / lt	late; late August/early September

The pastures were either grazed intensively twice a year (from mid-May to mid-June and from mid-August to mid-September) or extensively throughout the summer. Only sheep were used for grazing. Intensive grazing means having many animals per pasture during a short period (the more animals, the shorter the grazing period). Extensive grazing means few animals (max. 10 sheep/ha), but sufficient to consume the vegetation growth.

Combinations of mowing and grazing (hay-pastures)
In hay-pastures hay-making either occurred in early June followed by intensive grazing from mid-August to mid-September, or intensive grazing from mid-May to mid-June was followed by hay-making in September.

One trial plot of 32 m length was burnt every year in February and one trial plot of 8 m length was left unmanaged during the experiment.

2.3 SUMMARIZING OVERVIEW OF THE EXPERIMENTAL SET-UP

Table 8. Distribution of permanent quadrats over the various treatments (i.e. method of reconstruction, sowing and management).

Management		2xM	2xM	2xM	1xM	1xM	1xM2	1xM2	M+G	G+M	2xG	Gex	Br	0	Tot
Mowing time		e l	e l	e l	l	e	l	e	e	l					
Mowings		+ +	- -	+ -	+	+	+	+	+	+					
Recon.	Sowing														
SZ	1	3	2	1	2	1	2	1	1	1	1	1	.	.	16
SOD	1	1	1	.	1	.	1	.	.	.	.	.	.	.	4
RTS a	4	1	1	.	1	.	1	.	.	.	1	.	.	.	5
a	4	2	2	1	2	2	1	.	1	1	.	1	1	.	14
b	4	1	1	.	1	.	1	.	.	.	1	.	.	.	5
b	4	4	3	1	3	1	3	1	1	1	1	.	.	.	19
c	4	1	1	.	1	.	1	.	1	1	1	1	.	1	9
d	1	5	3	2	3	2	1	.	1	1	1	.	.	.	19
d	2	1	1	.	1	.	1	.	1	1	1	.	.	.	7
d	4	1	1	.	1	.	1	.	1	1	1	1	.	1	9
d	5	2	2	.	2	1	2	.	2	2	.	2	.	.	15
d	7	1	1	.	1	.	1	.	1	1	1	.	.	.	7
d	8	1	1	.	1	.	1	.	1	1	1	.	.	.	7
RSS	1	5	3	2	3	2	1	.	1	1	1	.	.	.	19
	2	1	1	.	1	.	1	.	1	1	1	.	.	.	7
	5	1	1	.	1	1	1	.	1	1	.	1	.	.	8
	6	1	1	.	1	.	1	.	1	1	.	1	.	.	7
	7	1	1	.	1	.	1	.	1	1	1	.	.	.	7
	8	1	1	.	1	.	1	.	1	1	1	.	.	.	7
IC	3	1	1	.	1	.	1	.	1	1	1	1	.	1	9
	4	16	14	3	14	6	13	2	5	5	6	5	1	.	90
	5	2	2	.	2	.	2	.	2	2	.	2	.	.	14
Total		53	45	10	45	16	39	4	25	25	21	16	2	3	304

In total 304 permanent plots were laid out on the experimental dike. Table 8 shows their distribution over the various treatments (i.e. method of reconstruction, sowing, management). See table 7 for explanation of the codes. Table 9 also shows the overall scheme, this time omitting the origin of the replacement topsoil and where it was replaced. Table 10 is even more simplified; it also omits the sowing treatments.

Table 9. Distribution of the permanent quadrats over the various treatments (method of reconstruction, sowing and management), omitting the origin of the replacement topsoil and where it was replaced.

Management		2xM	2xM	2xM	1xM	1xM	1xM2	1xM2	M+G	G+M	2xG	Gex	Br	0	Tot
Mowing time		e l	e l	e l	l	e	l	e	e	l					
Mowings		+ +	- -	+ -	+	+	+	+	+	+					
Recon.	Sowing														
SZ	1	3	2	1	2	1	2	1	1	1	1	1	.	.	16
SOD	1	1	1	.	1	.	1	.	.	.	.	.	.	.	4
RTS	1	5	3	2	3	2	1	.	1	1	1	.	.	.	19
	2	1	1	.	1	.	1	.	1	1	1	.	.	.	7
	4	10	9	2	9	3	8	1	4	4	5	3	1	2	61
	5	2	2	.	2	1	2	.	2	2	.	2	.	.	15
	7	1	1	.	1	.	1	.	1	1	1	.	.	.	7
	8	1	1	.	1	.	1	.	1	1	1	.	.	.	7
RSS	1	5	3	2	3	2	1	.	1	1	1	.	.	.	19
	2	1	1	.	1	.	1	.	1	1	1	.	.	.	7
	5	1	1	.	1	1	1	.	1	1	.	1	.	.	8
	6	1	1	.	1	.	1	.	1	1	.	1	.	.	7
	7	1	1	.	1	.	1	.	1	1	1	.	.	.	7
	8	1	1	.	1	.	1	.	1	1	1	.	.	.	7
IC	3	1	1	.	1	.	1	.	1	1	1	1	.	1	9
	4	16	14	3	14	6	13	2	5	5	6	5	1	.	90
	5	2	2	.	2	.	2	.	2	2	.	2	.	.	14
Total		53	45	10	45	16	39	4	25	25	21	16	2	3	304

Table 10. Distribution of the permanent quadrats over the various treatments, omitting the origin of replacement topsoil, where it was replaced and the sowing treatment applied.

Management	2xM	2xM	2xM	1xM	1xM	1xM2	1xM2	M+G	G+M	2xG	Gex	Br	0	Tot
Mowing time	e l	e l	e l	l	e	l	e	e	l					
Mowings	+ +	- -	+ -	+	+	+	+	+	+					
spared zone	3	2	1	2	1	2	1	1	1	1	1	-	-	16
sods	1	1	-	1	-	1	-	-	-	-	-	-	-	4
topsoil	20	17	4	17	6	14	1	10	10	9	5	1	2	116
subsoil	10	8	2	8	3	6	-	6	6	4	2	-	-	55
imp. clay	19	17	3	17	6	16	2	8	8	7	8	1	1	113
Total	53	45	10	45	16	39	4	25	25	21	16	2	3	304

2.4 STATISTICAL METHODS

Univariate statistics

Analysis of Variance (ANOVA: see Hair *et al.*, 1992; Kent & Coker, 1992) was used to explore separately the relationship between several environmental factors (e.g. soil parameters) and several other parameters (e.g. species richness, biomass production, root length) and plant communities, methods of reconstruction, sowing mixtures and management practices.

A basic assumption required for the validity of the significance tests in ANOVA is an univariate normal distribution of sample groups. All data sets of the above mentioned dependent and independent variables were tested on skewness by measuring the statistic value z (Hair *et al.*, 1992):

$$\mathbf{z = Skewness} \, / \, \sqrt{6/N}$$

where N is the sample size. If the calculated value exceeds a critical value, then the distribution is nonnormal. The critical value is from a z distribution, based on the desired significance level. For example, a calculated value exceeding ± 2.58 indicates that the assumption about normality of the distribution at the .01 probability level can be rejected. Another commonly used critical value is ± 1.96, which corresponds to a .05 error level.

Most of the distributions of the data sets were normal or approximated to normality. Only the distributions of the data of one of the factors related to the erosion resistance and all light parameters measured in the light penetration research were skewed. Therefore, these data sets were normalised by logarithm (LOG10) transformation.

Significant differences between contrasts are indicated by means of homogeneous groups. Homogeneous groups are described by characters. A homogeneous group contains treatments of which the mean values of the measured parameters do not significantly differ. Treatments which are significally different are assigned to different homogeneous groups. Homogeneous groups with one or more characters in common are not significantly different. Differences are tested with a oneway ANOVA followed by a Least Significance Difference (LSD) test.

Correlation analysis

Pearson product-moment correlation with two-tailed probabilities (see Hair *et al.*, 1992; Kent & Coker, 1992) was used to determine the relation between separate environmental factors (chapter 5), factors directly concerning the vegetation (e.g. species richness and biomass production) (chapters 3 and 5) and factors related to the erosion resistance (chapter 6). The Pearson correlation coefficient (r) indicates the strength of the association between the dependent and independent variables. The coefficient of determination (r^2) measures the proportion of the variance of the dependent variable about its mean that is explained by the independent, or predictor, variables. If the regression model is properly applied and estimated, the higher the value of r^2, the greater the explanatory power of the regression equation, and therefore the better the prediction of the criterion variable. Degrees of freedom provide a measure of how restricted the data are to reach a level of prediction. A large degrees-of-freedom value indicates that the prediction is fairly robust with regard to being representative of the overall sample of respondents. Conversely, a small degrees-of-freedom value suggests that the resulting prediction may be less generalizable, since few observations were not incorporated in the prediction. The Pearson product-moment correlation coefficient is based on certain assumptions about the data to which it is applied. First, data must be continuous and measured on either the interval or ratio scales. Second, each set of data should fit the normal distribution. In the case of the data of the dependent and independent variables considered in this study, most of the distributions were normal or approximated to normality (see also *univariate statistics*, mentioned above). Only the distributions of a few data sets were somewhat skewed. Therefore, these data sets were normalised by logarithm (LOG10) transformation.

Multivariate statistics
Two-way indicator species analysis (TWINSPAN) was used for classification of the vegetation (Hill, 1979b). Detrended correspondence analysis (DECORANA) was used to ordinate the relevés (permanent plots) (Hill, 1979a). The relation between plant communities and environment factors was determined by interpretation of the ordination diagrams. Therefore, the Pearson product-moment correlation between the ordination axes and the environmental factors was calculated.

2.5 SHORTCOMINGS IN THE EXPERIMENTAL SET-UP

In a part of section G2, in which a strip of the original vegetation was to be spared, a bend in the dike was straightened out and therefore no zone remained spared (i.e. sub-section G2'). However, on this part of the dike many species that otherwise occurred only in the spared zone were found in the first year of the experiment. Some of the topsoil originating from the zone originally earmarked to be spared appears to have been used for the new finishing layer. This deviating method of reconstruction should be considered separately when discussing the results.

The experimental dike was reconstructed a year before the research started. Because of this, there are some uncertainties about the methods of reconstruction applied. For instance in the lower part of section D2, where imported clay was used for the new top layer, many species of the former vegetation were found in the first year after the reconstruction. These species were represented in the upper part of section D2, where the former topsoil was used for the new top layer. When giving the finishing touch of the reconstruction some topsoil with propagules of the former vegetation was spread over the imported clay. For this reason the method of reconstruction of the lower part of section D2 was not considered to be imported clay but replaced topsoil. Besides this uncertainty, there is some uncertainty about the sowings applied, notably about the density of some sowings, which was not known exactly. Given the extensive set-up of the experiment, it is hardly possible to replicate the factor 'dike'. In this sense, the experiment is not replicated.

Last but nut least should be mentioned that the permanent plots were unequally distributed over the different methods of reconstruction, the different sowings applied and the different management practices (unbalanced design). Significance of differences is tested with a oneway ANOVA followed by a Least Significance Difference (LSD) test. In this LSD test the different numbers of samples are taken into account.

CHAPTER 3

CHANGES IN THE FLORISTIC COMPOSITION OF THE VEGETATION ON A RECONSTRUCTED RIVER DIKE BETWEEN 1987 AND 1994

With K.V. Sýkora

3.1 INTRODUCTION

In the Netherlands, the average amount of inorganic nitrogen fertilizer on grassland increased from 50 kg per ha in 1959 to 400 kg in 1980 (van Burg *et al.*, 1981). As a consequence unproductive species-rich grassland communities changed into productive grasslands, dominated by a few plant species. The general eutrophication had a negative impact on the former species-rich communities growing on the Dutch river dikes as well. Furthermore, these botanically valuable grasslands have been adversely affected by large-scale reconstructions (see Chapter 1). There is a need to restore the poorly productive species-rich grasslands in Europe, because they are deteriorating in quality and dwindling. The European Community is therefore now stimulating both restoration and management of these grasslands (Park, 1988). A great deal is already known about the functioning and management of low-productive, species-rich grasslands (Duffey *et al.*, 1974; Rorison & Hunt, 1980). However, less is known about how to restore these communities, i.e. how to develop them, for example after the reconstruction of river dikes.

The immigration of plant species by seed dispersal (Verkaar *et al.*, 1983b; Marshall, 1988) is an important regeneration characteristic, as are germination and seedling establishment (Grubb, 1977; Bakker *et al.*, 1980; Silvertown, 1981; Verkaar *et al.*, 1983a). Generally, the seedbank is removed during the reconstruction of river dikes. Consequently, species have to immigrate from the surrounding area. As species-rich river dike vegetation is very rare nowadays, there are usually few seed sources nearby, which hampers the immigration of new species and means that the vegetation development on reconstructed dikes often takes a very long time.

In this study various methods for reintroducing species directly after the reconstruction were investigated. In the first place *sparing a part of the vegetation* can provide a source from which species can disperse to the reconstructed parts of the dike. Secondly, *replacing the former top layer* which contains propagules of the former vegetation, can accelerate the vegetation development. The former top layer can be replaced manually as complete sods or by machine as loosened topsoil. Applying seed mixtures collected from the former vegetation just before the reconstruction can also accelerate the vegetation development.

Germination and seedling establishment is influenced by a variety of environmental factors (e.g. Silvertown, 1980, 1981; Fenner, 1987; Masuda & Washitani, 1990). Furthermore, the canopy structure of the vegetation, which determines both light penetration to the soil surface and microclimate, appears to be an important determinant of the onset of germination and seedling establishment (Oomes & Elberse, 1976; Verkaar *et al.* 1983a; Fenner, 1985; Goldberg, 1987).

3.2 METHODS

In order to restore former species-rich plant communities on an experimental river dike several methods of reconstruction were applied. The impact of the methods of reconstruction was investigated by describing the vegetation succession. Several species attributes and community characteristics were used to describe and explain successional sequences, such as species richness, syntaxonomical composition and proportion of rare species.

3.2.1 Analysis of the vegetation

Braun-Blanquet relevés

As noted in other chapters, the vegetation development was studied from 1987 to 1994 in relevés of 209 permanent plots $(6 \times 4m)^2$. The Braun-Blanquet method was used to analyse the vegetation in these permanent plots (Westhoff & Van der Maarel, 1973). The phanerogams were named according to Van der Meijden (1990). A modified version of the Braun-Blanquet scale (Barkman *et al.*, 1964) was used to express the species abundance. The modification enabled differences between 1, 2 and 3 individuals of a species to be expressed. Table 11 shows the scale used after ordinal trans formation (according to Van der Maarel, 1979). The permanent plots were positioned in the middle of each trial plot, vertically always at the same place in the gradient. The vegetation development was studied on the basis of vegetation data of 4 years. In 1987 169 relevés were made; in 1990 205; in 1992 225 and in 1994 209. The reason of the low number of relevés in 1987 was that the research only started in July of that year.

Table 11. Ordinal scale used to represent species abundances in the Braun-Blanquet relevés, and explanation of the codes.

Ordinal scale	Braun-Blanquet scale *abundance*	*%-cover*
1	1 individual	< 5
2	2 individuals	< 5
3	3 to 10 ind.	< 5
4	10 or more ind.	< 5
5	not relevant	5 - 12.5
6	ditto	12.5 - 25
7	ditto	25 - 50
8	ditto	50 - 75
9	ditto	75 - 100

3.2.2 Synthesis

Both cluster and ordination techniques were used to study the multidimensional variation in the vegetation data and additionally to analyse the spatial and temporal development of the vegetation. TWINSPAN (Hill, 1979b; Gauch, 1982; Kershaw & Looney, 1985) was used for clustering, DECORANA (Hill, 1973, 1979a; Gauch, 1982; Kershaw & Looney, 1985) for ordination.

Plant communities

Initially, 76 groups of relevés (clusters or vegetation units) were distinguished within the 808 relevés, based on the TWINSPAN table and the ordination diagrams constructed by means of DECORANA. Centroids, i.e. the sum of the cover-abundance values of a species in a cluster devided by the total number of relevés in this cluster, were calculated for the 76 groups of relevés. These 76 centroids were clustered and ordinated again. Based on the results the most similar vegetation units were combined into 18 new vegetation units. These 18 centroids were clustered and ordinated again, a synoptic table was made and the syntaxonomical composition of the vegetation units was analysed. Again the most similar units were combined and finally 9 plant communities were distinguished.

Synoptic table

The communities distinguished were presented in a synoptic table (Westhoff & Van der Maarel, 1973), in which relevés assigned to the same plant community are summarized in one column. The frequency of occurrence of the species was given in roman numerals and the mean abundance in arabic numerals (superscript). In the synoptic table the species were grouped into the major syntaxonomical elements (see appendix 1 at page 61). Species whose frequency is at least 30% higher than in the other plant communities are considered to be differential. In table 16 the differential species have been boxed, as have

Table 12. Explanation of codes for frequency.

Class	Frequency
+	0 - 5 %
I	6 - 20 %
II	21 - 40 %
III	41 - 60 %
IV	61 - 80 %
V	81 - 100 %

species which are differential for more than one vegetation unit. The syntaxonomical elements were named according to Westhoff & Den Held (1969). The plant communities were named on the basis of the proportions of the most important syntaxonomical elements and using two characteristic species, which were usually also differential.

Van der Zee (1992) distinguished 22 plant communities on dikes in the Netherlands. Nine occurred exclusively on the dikes of the rivers Rhine, Waal and Meuse, and 6 occurred exclusively on the dikes of the Juliana canal. The other communities were found on sea dikes and on dikes which are no longer used as primary dikes. The latter are mostly situated in the province of Zeeland. A qualitative version of the SØRENSEN index of similarity I_S (see Kent & Coker, 1992) was used to determine the resemblance of those plant communities with the communities distinguished in this study. This qualitative index is based solely on presence/absence data of species.

3.2.3 Characteristics of the plant communities

The following attributes were used to compare the plant communities: mean number of species; proportions (%) of syntaxonomical elements; proportions (%) of the syntaxonomical elements within the *Molinio-Arrhenatheretea;* frequency and mean abundance of the characteristic species of the *Arrhenatheretum elatioris;* presence of stream valley plants; proportions (%) of the national rarity categories in 1980; average indicator value (AIV) for soil fertility; peak standing crop.

Syntaxonomical elements

Most plant species can be assigned to one or more syntaxonomical elements (according to Westhoff & Den Held, 1969). In this way 31 syntaxonomical elements were distinguished. Many of them were represented by only a few species which, in addition, had a low abundance. For this reason all elements were grouped into 12 main elements (table 13).

Table 13. Main syntaxonomical elements.

Class	*Molinio-Arrhenatheretea*
Order	*Molinietalia*
Alliance	*Arrhenatherion elatioris*
Association	*Arrhenatheretum elatioris*
Association	*Lolio-Cynosuretum*
Class	*Koelerio-Corynephoretea & Festuco-Brometea*
Class	*Trifolio-Geranietea sanguinei*
Alliance	*Trifolion medii*
Class	*Plantaginetea majoris*
Class	*Artemisietea vulgaris*
Class	*Chenopodietea*
Class	*Secalietea*
Other	*species not characteristic of one of above mentioned syntaxa*

Table 14 shows the syntaxonomical elements that were distinguished within the class *Molinio-Arrhenatheretea*. It also shows the sub-associations distinguished within the *Arrhenatheretum elatioris* and the *Lolio-Cynosuretum*.

Table 14. Syntaxonomical elements within the Molinio-Arrhenatheretea.

Class	*MOLINIO-ARRHENATHERETEA*
Order	*Molinietalia*
Alliance	*Arrhenatherion elatioris*
Association	*Arrhenatheretum elatioris*
sub-association group A	
sub-association group B	
sub-association	*brizetosum*
sub-association	*picridetosum*
Association	*Lolio-Cynosuretum*
sub-association group A	
sub-association	*luzuletosum campestris*
sub-association group B	
sub-association	*ononidetosum*
sub-association	*plantaginetosum mediae*

Stream valley plants

The fluviatile district is floristically very well characterized (Van der Meijden, 1990). Many species are restricted to this district or to only one or two other districts as well. They are called stream valley plants. The presence of the stream valley plants in the distinguished plant communities was investigated.

Rarity categories

The national rarity categories (i.e. n.r.c.) indicate the rarity of the species in the Netherlands in 1980. The rarity is expressed as the estimated number of grid cells of 5km x 5km, in which the species occurred in 1980 according to the 'Standard list of the Dutch flora 1984' (Van der Meijden *et al.*, 1984). Table 15 explains the codes of rarity.

Table 15. Explanation of codes of rarity of species in 1980. NRC = national rarity category.

NRC	Number of 5km x 5km grid cells	Meaning
0	0	extinct/not found
1	1 - 3	extremely rare
2	4 - 10	very rare
3	11 - 29	rare
4	30 - 79	fairly rare
5	80 - 189	less common
6	190 - 410	fairly common
7	411 - 710	common
8	711 - 1210	very common
9	1211 - 1677	extremely common

Ecological indicator values for soil fertility

When environmental data are scarce or absent, changes in the environment can often be inferred from changes in the vegetation, by means of known properties of the species involved. A species qualification with respect to the nutrient status of the soil was used for an indirect way of quantifying the variation between the plant communities (Klapp, 1965; Ellenberg, 1979). The average indicator value (AIV) for soil fertility of the species involved (Ellenberg, 1974) can be used as an expression of the fertility of the soil. Additionally, all species occurring on the experimental dike were subdivided into three groups ('poor', 'intermediate' and 'rich' species), indicating the nutrient status of the soils. Species with nitrogen values of 1 to 4, according to Ellenberg (1974), were grouped as 'poor' species and values of 7 to 9 as 'rich'. The ratio of number of species indicating nutrient-poor soils : number of species indicating nutrient-rich soils was used as a quantitative index of soil fertility. Another index was calculated by taking the abundance of the various species into account. Indifferent species, i.e. species without a clear indication of soil characteristics, and species with an unknown indicator value have been ignored.

Peak standing crop

The peak standing crop was used as an indication of the soil fertility. The relation between peak standing crop and species diversity was calculated (see also Chapter 5).

3.2.4 Development of the vegetation

The vegetation development was studied in two ways. First, the floristic composition at the start (1987) was compared with that at the end of the experiment (1994). Secondly, the vegetation in 1987, 1990, 1992 and 1994 was compared. To study the effect of the different methods of reconstruction, the different sowings and the different management practices 209 permanent plots were set out on the experimental dike. Sections A and B were reconstructed in 1987, a year later than sections C to G. Sections A and B together contained 37 permanent plots, the other sections contained 172 such plots.

Comparison between 1987 and 1994
The soil per reconstruction method was assumed to be homogeneous. The management practices were applied from 1987 onwards and therefore the vegetation had not yet been influenced by management in that year. Therefore in 1987, one year after the dike reconstruction, the vegetation composition was approximately homogeneous within each method of reconstruction but differed between methods of reconstruction. This means that the relevés within one method of reconstruction were very similar but relevés from different methods of reconstruction were less similar. Therefore, in 1987 the vegetation of each method of reconstruction could be described by only a few, representative relevés. Thus, in 1987 the vegetation in only 82 of 172 plots of sections C to G was analysed, but they represented the starting situations of all 172 permanent plots.

In 1988 the vegetation in all 37 permanent plots of sections A and B were analysed. So, the starting situation was represented by 209 relevés: 172 for 1987 and 37 for 1988. In 1994 the same 209 permanent plots were analysed. Consequently, the vegetation in 1987 and 1994 was compared by means of data from 209 permanent plots for both years. It should be noted that by 1994 the vegetation in sections A and B had been developing for 7 years, whereas in the other sections it had been developing for 8 years. This should be borne in mind when discussing the vegetation development.

The vegetation in 1987 and 1994 was compared in terms of the number of permanent plots belonging to the plant communities distinguished. If its vegetation composition changed sufficiently, a permanent plot was reassigned to the appropriate plant community. All such shifts were determined and counted; the number of permant plots that did not change community was also counted.

Ordination diagrams
Cluster centroids were calculated for relevés belonging to one plant community. The centroids of the 9 plant communities were ordinated by means of Detrended Correspondence Analysis (DCA) (Hill, 1979). The first 3 ordination axes were used to construct the diagrams. These 3 ordination axes were interpreted by means of proportions of syntaxonomical elements, of species characteristic of pastures or hay meadows, of species characteristic of nitrogen-poor or nitrogen-rich conditions and by species richness.

The Ellenberg indicator value for the nutrient status of the soil was used for the interpretation of the ordination axes (Klapp, 1965; Ellenberg, 1979). All species occurring on the experimental dike were subdivided into three groups ('poor', 'intermediate' and 'rich' species), indicating the nutrient status of the soils in which they normally occur. In this study species with nitrogen values of 1 to 4, according to Ellenberg (1979), were grouped as 'poor' species and values of 7 to 9 as 'rich'.

Succession trends
The shifts between the plant communities in the period 1987-1994 were represented by arrows in a succession scheme and in a kinematic graph which was based on the succession scheme. The arrow thickness increases with the frequency of the shifts. All possible succession trends including their frequencies were determined by analysing all observed shifts in plant communities and consequently grouping them, giving a few major shifts and several minor shifts.

Comparison of 1987, 1990, 1992 and 1994
The vegetation in 1987, 1990, 1992 and 1994 was compared by means of data from the 209 permanent plots in these years. The following attributes were used to compare the plant communities: mean number of species; proportions (%) of the 9 plant communities; proportions (%) of syntaxonomical elements; proportions (%) of the syntaxonomical elements within the *Molinio-Arrhenatheretea*; frequency and mean abundance of the characteristic species of the *Arrhenatheretum elatioris* and proportions (%) of the national rarity categories in 1980.

3.2.5 Comparison of the flora before and after the dike reconstruction

Flora before the dike reconstruction
Hardly any recent data were available on the dike flora before the reconstruction. However, the spared zone indicated what the vegetation looked like before reconstruction. Information on the former vegetation composition was obtained from the literature and other sources.

After making an inventory of the vegetation of Dutch river dikes, Neijenhuijs (1968) provided lists of only the more important plant species, whereas in an inventory by a local nature organization the grass species were omitted (Natuurwacht Zaltbommel, 1978). The only other information available consists of a few relevés made in 1984 and 1985 for a study on the civil engineering and ecological engineering aspects of river dike vegetation (Sýkora & Liebrand, 1987) and for an inventory made by the Province of Gelderland. These relevés represented the vegetation on only a few locations on the experimental dike before 1987. However, the fact that so few relevés were made before 1987 suggests that there was little variation in vegetation composition on the dike before the reconstruction. On the other hand, it can be expected that relevés tend to be made of the best developed vegetation, and therefore they will provide a good picture of the species which occurred before the reconstruction.

People living near the experimental dike were questioned about the management of the vegetation before the reconstruction. They said it had been irregular. Most parts of the dike had been mown twice a year, but parts difficult to reach - especially those on the lower parts of the dike - were often left unmown. The vegetation in these parts must have been very rough; this was confirmed by slides taken by Grontmij Consultancy just before the dike reconstruction. The mowings were only removed if the weather was favourable for hay-making, otherwise they were left in situ, as was done on almost all river dikes then. The slides taken by Grontmij Consultancy were snapshots of the vegetation at a certain moment, but from these it could be concluded that the former vegetation at the locations photographed was relatively productive and consisted of many tall, ruderal herbs such as *Heracleum sphondylium, Anthriscus sylvestris, Symphytum officinale, Calystegia convolvulus, Urtica dioica, Rumex obtusifolius, Rubus caesius* and *Cirsium arvense*. Species such as *Phragmites australis, Phalaris arundinacea, Valeriana officinalis* and *Filipendula ulmaria* also indicated ruderalization but also relatively damp conditions. *Arrhenatherum elatius, Dactylis glomerata, Alopecurus pratensis, Elymus repens* and *Phleum pratense* were probably the most frequent grass species. Plant species of greater botanical value could only be found sporadically, on intermittently well managed locations.

The similarity of the flora before and after the dike reconstruction was determined by comparing the species in the Braun-Blanquet relevés made from 1987 to 1994 with the data from the 1978 inventory done by a local nature organization (Natuurwacht Zaltbommel, 1978). Therefore, both the absence or presence of species and their frequency were analysed. Frequency was determined by dividing the number of plots in which a species was found by the total number of plots analysed. The frequency before and after reconstruction could be compared because in 1978 the frequency of the species had also been determined.

3.2.6 Statistics

ANOVA was used to explore separately the relationship between the dependent variables considered in this chapter and the independent variable plant community (see also § 2.4). All data sets were normally distributed. Differences are tested with a oneway ANOVA followed by a Least Significance Difference (LSD) test. Treatments which are significally different are assigned to different homogeneous groups. Homogeneous groups with one or more characters in common are not significantly different.

Pearson product-moment correlation with two-tailed probabilities was used to determine the relation between the Decorana axes and the syntaxonomical elements, the indicatieve species and the species richness.

3.3 Results

3.3.1 Plant communities

Between 1987 and 1994 the following 9 plant communities were distinguished on the experimental river dike[1] (for synoptic table; see appendix 1 on page 61):

- I *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus*
- II *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis*
- III *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia*
- IV *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense*
- V *Arrhenatheretum* with dominance of *Alopecurus pratensis*
- VI *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens*
- VII Association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens*
- VIII Fragmentary community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion elatioris/Eu-Polygono-Chenopodion*]
- IX Fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*]

Syntaxonomy and synecology

A *ARRHENATHERETUM ELATIORIS* (communities I - VIII)

Syntaxonomy
Communities I to VIII were assigned to the *Arrhenatheretum* because of the occurrence of the following characteristic species of the *Molinio-Arrhenatheretea*, the *Arrhenatherion and the Arrhenatheretum (see appendix 1): Cardamine pratensis, Centaurea jacea, Cerastium fontanum, Holcus lanatus, Plantago lanceolata, Prunella vulgaris, Rumex acetosa, Trifolium pratense* and *Vicia cracca* (*Molinio-Arrhenatheretea); Achillea millefolium, Alopecurus pratensis, Bellis perennis, Dactylis glomerata, Festuca pratensis, Heracleum sphondylium, Lathyrus pratensis, Leucanthemum vulgare, Lotus corniculatus, Ranunculus acris, Senecio jacobea, Taraxacum officinale* and *Trifolium dubium* (*Arrhenatherion); Arrhenatherum elatius, Crepis biennis, Daucus carota, Galium mollugo, Pastinaca sativa, Peucedanum carvifolia, Pimpinella major, Rumex thyrsiflorus, Tragopogon pratensis x orientalis* and *Trisetum flavescens* (*Arrhenatheretum*).

Aa *ARRHENATHERETUM ELATIORIS* sub-association group B (community I)

<u>Community I</u> *Arrhenatheretum elatioris* with *Peucedanum carvifolia* and *Rumex thyrsiflorus*

Syntaxonomy
In addition to containing two differential species of sub-association group B (*Senecio jacobea* and *Trisetum flavescens*), community I contained many differential species of the *picridetosum* sub-association (*Agrimonia eupatoria, Carduus crispus, Cichorium intybus, Pastinaca sativa, Peucedanum carvifolia* and *Tragopogon pratensis x orientalis*), some of which occurred with a rather high abundance. Community I has therefore been designated to sub-association group B of the *Arrhenatheretum*, and might be in the *picridetosum* sub-association. The following species were exclusively differential to community I (see table 16): *Convolvulus arvensis, Peucedanum carvifolia, Rumex thyrsiflorus, Tanacetum vulgare* and *Verbascum nigrum. Lamium album* was differential for the communities I and II together.

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[1] In 1996 Schaminée *et al.* published a new review of the plant communities of the grasslands. Adjustment to this review would merely change the names of the communities but would not affect the distinction into 9 communities. See also § 3.4.1.

Table 16. Synoptic table of the plant communities distinguished. The percentage presence is expressed in six classes: + = 0-5%; I = 6-20%; II = 21-40%; III = 41-60%; IV = 61-80%; V = 81-100%. The exclusive differential species and the species that are differential species of several communities together are boxed.

PLANT COMMUNITY	I	II	III	IV	V	VI	VII	VIII	IX
No. of relevés	66	61	89	23	226	203	117	18	5
Mean no. of species	32	27	42	39	29	32	26	26	35
Rumex thyrsiflorus	V	+	I	I	I	+	+	-	-
Tanacetum vulgare	IV	II	I	I	I	I	I	I	-
Convolvulus arvensis	IV	+	+	-	II	II	I	-	-
Peucedanum carvifolia	III	+	-	-	+	+	+	-	-
Verbascum nigrum	III	+	-	-	+	-	+	-	-
Lamium album	V	III	+	-	I	I	I	I	-
Alopecurus pratensis	IV	V	III	I	V	III	I	I	IV
Arrhenatherum elatius	V	V	V	V	V	V	IV	II	II
Dactylis glomerata	V	V	V	V	V	V	IV	III	I
Poa pratensis	III	II	IV	III	IV	IV	II	-	-
Elymus repens	V	V	V	V	V	V	IV	II	V
Rubus caesius	IV	IV	IV	III	II	II	II	-	III
Festuca rubra	V	IV	V	V	V	V	IV	V	-
Heracleum sphondylium	V	V	V	V	IV	III	II	II	-
Anthriscus sylvestris	V	V	V	III	IV	III	III	V	I
Achillea millefolium	IV	II	V	IV	II	II	II	III	-
Vicia cracca	IV	IV	V	V	IV	III	III	II	-
Poa trivialis	IV	IV	IV	IV	IV	IV	III	IV	I
Daucus carota	II	+	II	II	II	III	II	II	-
Phleum pratense	III	I	III	V	III	IV	V	V	IV
Ranunculus repens	II	+	IV	V	III	V	V	V	IV
Urtica dioica	III	V	II	-	II	I	I	-	-
Valeriana officinalis	-	III	III	I	+	+	+	-	-
Senecio erucifolius	-	II	II	III	+	+	-	-	-
Lysimachia nummularia	-	I	IV	II	II	I	+	I	-
Leucanthemum vulgare	-	+	IV	IV	I	II	I	-	-
Trifolium pratense	I	+	IV	V	III	V	IV	IV	-
Trifolium repens	I	-	IV	V	II	V	V	V	IV
Crepis capillaris	+	-	I	I	I	III	I	-	-
Plantago major	+	-	I	II	+	II	III	V	-
Matricaria maritima	I	+	I	II	+	I	III	V	III
Polygonum aviculare	+	-	-	-	+	I	II	V	V
Chenopodium album	+	-	+	+	+	+	I	IV	V
Matricaria discoidea	-	-	-	-	-	-	-	II	III
Matricaria recutita	-	-	-	-	+	+	+	II	II
Stellaria media	II	I	I	+	I	I	II	III	V
Capsella bursa-pastoris	I	-	+	+	+	+	II	III	V
Sinapis arvensis	-	I	I	I	I	+	I	II	V
Rorippa sylvestris	-	-	-	I	+	+	I	II	V
Poa annua	-	-	-	-	+	I	I	I	V
Euphorbia helioscopia	-	-	-	-	+	+	+	-	V
Lamium purpureum	-	-	-	-	+	+	-	-	V
Polygonum persicaria	+	-	+	+	-	+	I	II	IV
Senecio vulgaris	+	-	+	+	+	+	I	I	III
Brassica nigra	-	+	+	-	+	-	-	-	II
Solanum nigrum	-	-	-	-	-	-	+	-	II
Veronica arvensis	-	-	-	-	-	-	-	-	II

Ab *ARRHENATHERETUM ELATIORIS* sub-association group A (communities II - VIII)

In spite of the presence of a number of differential species of sub-association group B, the species which are differential of sub-association group A dominated. The following differential species, whose occurrence enables sub-association group A to be distinguished from sub-association group B occurred in communities I to VIII: *Alopecurus pratensis*, *Anthriscus sylvestris*, *Glechoma hederacea*, *Heracleum sphondylium* and *Ranunculus repens*. Nearly all species differential of the *alopecuretosum* sub-association were found: *Cardamine pratensis*, *Lysimachia nummularia*, *Ranunculus ficaria* and *Symphytum officinale*. However, almost all of them had a low abundance and therefore this vegetation could be assigned to the *inops* sub-association.

The following species which are differential of sub-association group B or one of the sub-associations of this group were found in communities I to VIII: *Plantago media*, *Ranunculus bulbosus*, *Senecio erucifolius*, *Senecio jacobea* and *Trisetum flavescens*. These species together with *Agrimonia eupatoria*, *Carduus crispus*, *Cichorium intybus*, *Pastinaca sativa*, *Peucedanum carvifolia* and *Tragopogon pratensis x orientalis* are an element of the *picridetosum* sub-association of sub-association group B. Because these species occurred sporadically and with low abundance in communities II to VIII, these communities were retained in sub-association group A.

A lack of character species made it difficult to assign communities VII and VIII at the association level. However, the species that were present made inclusion of community VII in the *Arrhenetheretum* association justifiable. It was assigned as an association fragment[2]. Community VIII was determined as a transition between the *Eu-Polygono-Chenopodion* and the *Arrhenatherion elatioris*.

Urtica dioica is the only exclusive differential species of community II (see table 16). *Valeriana officinalis* distinguishes communities II and III from the other communities. *Lamium album* distinguishes communities I and II from the other communities. *Lysimachia nummularia* is the only exclusive differential species of community III. Community IV has no exclusive differential species. *Leucanthemum vulgare* distinguishes communities III and IV from the other communities. Community V has no differential species. *Crepis capillaris* is the only exclusive differential species of community VI. Because of a relatively low proportion of *Arrhenatheretum* species and relatively high proportions of *Lolio-Cynosuretum* and *Plantaginetea* species community VI is assigned as a transition between *Arrhenatheretum* and *Lolio-Cynosuretum* (see table 18). To distinguish this community from the other *Arrhenatheretum* communities it henceforth is called a *Lolio-Cynosuretum* community. Community VII has no differential species. *Matricaria maritima* and *Plantago major* are exclusive differential species of community VIII. *Chenopodium album*, *Matricaria discoidea*, *Matricaria recutita* and *Polygonum aviculare* distinguish communities VIII and IX from the other communities.

B *EU-POLYGONO-CHENOPODION* (community IX)

Community IX Fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*]

Syntaxonomy

Community IX was assigned to the *Eu-Polygono-Chenopodion* because of the occurrence of the following characteristic species of the *Chenopodietea* and the *Eu-Polygono-Chenopodion*: *Capsella bursa-pastoris*, *Chenopodium album*, *Senecio vulgaris*, *Solanum nigrum*, *Sonchus asper*, *Sonchus oleraceus* and *Stellaria media* (*Chenopodietea*); *Euphorbia helioscopia*, *Geranium dissectum*, *Lamium purpureum*, *Polygonum persicaria*, *Sonchus asper*, *Veronica agrestis* and *Veronica persica* (*Eu-Polygono-Chenopodion*). *Brassica nigra*, *Capsella bursa-pastoris*, *Euphorbia helioscopia*, *Lamium purpureum*, *Poa annua*, *Polygonum persicaria*, *Rorippa sylvestris*, *Senecio vulgaris*, *Sinapis arvensis*, *Solanum nigrum*, *Stellaria media* and *Veronica arvense* are exclusive differential species of community IX (see table 16). *Chenopodium album*, *Matricaria discoidea*, *Matricaria recutita* and *Polygonum aviculare* distinguish communities VIII and IX from the other communities.

3.3.2 Characteristics of the plant communities

Species diversity

The mean species diversity of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) and the *Arrhenatheretum with Leucanthemum vulgare* and *Trifolium pratense* (IV) was significantly higher ($p<0.05$) than that of the other communities (see table 17).

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[2] Association fragments are phytocoena in which some percentage of the species combination characteristic of a given association is lacking, and the species that are present make inclusion in this association justifiable (Kopecký & Hejný, 1974; Schaminée *et al.*, 1990).

Table 17. Species diversity of the plant communities. Total number of species, number of herbs and forbs and number of grasses and grassy species. Homogeneous groups at p<0.05 level.

Plant comm.	Number of species	Homogen. groups	Plant comm.	Herbs+ forbs	Homogen. groups	Plant comm.	Number of grasses	Homogen. groups
III	41.7	a . . .	III	31.3	a . .	III	10.3	a . . . . .
IV	39.0	a . . .	IV	29.7	a . .	VI	9.4	. b . . . .
IX	34.6	. b . .	IX	29.4	a . .	IV	9.4	. b c . . .
VI	32.4	. b . .	VI	23.0	. b .	I	8.9	. b c . . .
I	31.7	. b . .	I	22.8	. b .	V	8.9	. . c . . .
V	29.0	. . c .	VIII	20.7	. b c	II	8.1	. . . d . .
II	27.4	. . c d	V	20.1	. . c	VII	6.6	. . . . e .
VII	26.4	. . . d	VII	19.7	. . c	VIII	5.3	. . . . . f
VIII	25.9	. . . d	II	19.3	. . c	IX	5.2	. . . . . f

The mean number of herbs and the mean number of grasses were both largest in community III. Moreover, the species diversity of the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I), the *Lolio-Cynosuretum with Crepis capillaris* and *Ranunculus repens* (VI) and the fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) was significantly higher than that of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II), the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V), the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) and the fragmentary community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII). Community II had the least number of herbs. The early successional stages, communities VII-IX, contained a relatively small number of grasses.

Syntaxonomical elements

Table 18. Relative importance (%) of the main syntaxonomical elements in the plant communities.

Syntaxonomical elements	Plant communities I	II	III	IV	V	VI	VII	VIII	IX
Molinio-Arrhenatheretea & Arrhenatherion	23.2	24.8	34.2	30.8	30.6	31.5	24.0	16.5	13.7
Arrhenatheretum	29.2	28.4	22.8	16.0	25.5	18.7	11.5	7.9	3.2
Lolio-Cynosuretum	12.0	6.0	11.5	14.9	11.7	15.4	16.6	16.5	5.0
Koel-Coryn & Fest-Brom*	2.2	.3	.8	.2	.2	.2	.1	.1	.7
Trifolion medii	1.2	.8	.4	1.2	.0	.0	.0	.0	.0
Artemisietea	13.9	19.3	9.2	8.5	10.0	7.2	7.9	4.9	6.1
Plantaginetea	3.1	.9	5.8	12.0	5.5	12.0	21.3	30.6	18.9
Chenopodietea	3.1	4.3	3.8	5.3	3.3	3.4	8.5	17.9	41.2
Overige	11.9	15.3	11.5	11.3	13.3	11.6	10.0	5.7	11.3

* Koelerio-Corynephoretea & Festuco-Brometea

Table 18 shows the relative importance of the main syntaxonomical elements. *Molinio-Arrhenatheretea* species mainly occur in hay meadows (*Arrhenatheretum*), permanent pastures (*Lolio-Cynosuretum*) and grasslands with a combination of hay-making and grazing management (transitions between *Arrhenatheretum* and *Lolio-Cynosuretum*). The differential species of the *Koelerio-Corynephoretea* together with the *Festuco-Brometea* are characteristic of herbaceous vegetations of sand dunes and other sandy soils. *Trifolion medii* species often occur in forb fringes, taking an intermediate position between grassland and forest. The *Artemisietea* element consists of species of nitrophilous tall herb weed communities of marginal areas and relatively stable, formerly disturbed ground. The *Plantaginetea* are typical of trampled areas and artificially compacted soils. The *Chenopodietea* comprise nitrophilous pioneer communities of arable fields and ruderal waste places.

The fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) differed most from the other communities. The proportion of the *Molinio-Arrhenatheretea* together with the *Arrhenatherion*, the *Arrhenatheretum* and the *Lolio-Cynosuretum* was relatively small, whereas the proportion of the *Chenopodietea* (together with the *Secalietea*) was relatively large. This vegetation mainly consisted of annual pioneer species. The proportion of the *Arrhenatheretum* was the largest in the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) and in the *Arrhenatheretum with Urtica dioica* and *Valeriana officinalis* (II). Whereas community I contained relatively many species of the *Koelerio-Corynephoretea* and the *Festuco-Brometea* and the *Trifolion medii*, in community II the *Artemisietea* was the largest element. So community I consisted of an *Arrhenatheretum* vegetation with species that prefer dry condions, and community II of an *Arrhenathererum* vegetation with many ruderal species.

In the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) and the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) the proportion of the syntaxonomical elements did not differ appreciably. In contrast with communities I, II, III and V, in the *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV) the *Arrhenatheretum* and the *Lolio-Cynosuretum* were present in almost equal proportions. In addition, community IV had a relatively large proportion of the *Plantaginetea*, and was therefore determined as a meadow community clearly influenced by grazing. The *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) resembled community IV. However, species of the *Trifolion medii* were missing from community VI.

The association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) and the fragmentary community of the *Arrhenatheretum with Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) both contained some *Lolio-Cynosuretum* species, but the proportion of the *Plantaginetea* and the *Chenopodietea* was larger in community VIII than in community VII.

Syntaxonomical elements belonging to the Molinio-Arrhenatheretea

The proportion of species characteristic of the *Arrhenatheretum* was largest in the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) and smallest in the fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) (see tables 18 and 19).

Table 19. Percentages of the syntaxonomical elements of the Molinio-Arrhenatheretea within the plant communities.

Syntaxonomical elements	Plant communities I	II	III	IV	V	VI	VII	VIII	IX
Molinio-Arrhenatheretea	11.4	11.4	17.1	15.2	15.0	15.7	12.3	8.5	6.1
Molinietalia	.0	1.5	1.2	.5	.1	.1	.1	.1	.0
Arrhenatherion	11.5	11.9	15.7	14.9	15.1	14.8	11.5	7.8	7.0
Arrhenatheretum	15.6	12.2	9.5	7.8	12.8	9.6	5.5	2.5	1.1
subass.group A	10.4	15.8	11.2	7.4	10.2	5.4	4.6	4.2	1.6
subass.group B	1.0	1.1	1.9	1.8	1.3	1.9	.3	.1	.5
brizetosum	.3	.0	.6	.1	.7	1.8	.8	.4	.0
picridetosum	3.5	.8	.6	.6	1.1	1.4	1.4	1.0	1.4
Lolio-Cynosuretum	1.9	.6	2.7	4.0	2.0	3.4	6.2	7.3	3.2
subass.group A	4.9	3.1	3.8	3.5	4.5	4.5	4.8	6.6	.0
subass.group B	2.7	2.3	3.6	4.7	3.5	4.4	2.7	.6	1.4
ononidetosum	2.6	.1	1.3	2.6	1.6	3.1	2.9	2.1	.5
Other	34.3	39.3	30.8	36.9	32.1	34.0	47.0	59.0	77.5

The proportion of sub-association group A of the *Arrhenatheretum* was largest in the rough *Arrhenatheretum* vegetation with *Urtica dioica* and *Valeriana officinalis* (II). The proportion of the *picridetosum* sub-association of sub-association group B of the *Arrhenatheretum* was largest in the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I). The proportion of the *brizetosum* sub-association of sub-association group B of the *Arrhenatheretum* was relatively small in all communities, but was largest in the transition between the *Arrhenatheretum* and the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI). The proportion of the *Lolio-Cynosuretum* was smallest in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) and the fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) and did not differ much in the other communities (see tables 18 and 19). The proportion of the *ononidetosum* element was largest in the transition between the *Arrhenatheretum* and the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI).

Characteristic species of the Arrhenatheretum elatioris

The weighted frequency and the weighted abundance of the species characteristic of the *Arrhenatheretum* both showed that community I, the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus*, was the best developed *Arrhenatheretum* (see table 20).

Table 20. Frequency (%) and mean cover abundance (ordinal scale; superscript) of the characteristic species of the Arrhenatheretum elatioris in the plant communities.

Characteristic species of the Arrhenatheretum elatioris	Plant communities								
	I	II	III	IV	V	VI	VII	VIII	IX
Arrhenatherum elatius	100^{8}	100^{8}	98^{7}	95^{5}	98^{8}	96^{6}	65^{3}	27^{1}	40^{1}
Crepis biennis	19^{1}	6^{1}	47^{2}	65^{2}	36^{1}	28^{1}	17^{1}	.	.
Daucus carota	37^{1}	3^{1}	23^{1}	34^{1}	33^{1}	58^{2}	25^{1}	38^{1}	.
Galium mollugo	90^{4}	80^{3}	75^{3}	56^{2}	61^{2}	59^{2}	22^{1}	.	20^{1}
Pastinaca sativa	12^{1}	.	1^{1}	.	9^{1}	3^{1}	4^{1}	33^{1}	.
Peucedanum carvifolia	51^{2}	1^{1}	.	.	3^{1}	1^{1}	3^{1}	.	.
Pimpinella major	.	.	.	.	.	1^{1}	.	.	.
Rumex thyrsiflorus	80^{3}	3^{1}	6^{1}	8^{1}	5^{1}	1^{1}	3^{1}	.	.
Tragopogon prat. ssp. or.	27^{1}	.	11^{1}	8^{1}	13^{1}	4^{1}	7^{1}	5^{1}	.
Trisetum flavescens	22^{1}	8^{1}	8^{1}	.	11^{1}	6^{1}	2^{1}	.	.
means	44^{2}	20^{2}	27^{2}	27^{1}	27^{2}	26^{1}	15^{1}	10^{1}	6^{1}

Although the species composition of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III), the *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV), the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) and the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) differed strongly, the proportion of species characteristic of the *Arrhenatheretum* was about the same. The fragmentary community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) was the most fragmentary. In the fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) only two characteristic species of the *Arrhenatheretum* occurred, and these had a very low abundance. Two characteristic species of the *Arrhenatheretum elatioris* (according to Westhoff & Den Held, 1969), *Geranium pratense* and *Knautia arvensis*, were found in none of the plant communities. The first species was never found on the experimental dike whereas before the reconstruction the second species was only found on one location and in a very low number.

Stream valley plants

The following species found on the experimental dike are restricted to the fluviatile district (F): *Peucedanum carvifolia*, *Rumex thyrsiflorus* (neophyte) and *Tragopogon pratensis ssp. orientalis*. Restricted to F and the 'Zuidlimburgs' district (Z) are: *Crepis biennis*, *Cruciata laevipes* and

Leontodon hispidus. Restricted to F, Z and the Estuarine district (E) are: *Pimpinella major*, *Senecio erucifolius*, *Trisetum flavescens* and *Verbena officinalis*. *Medicago falcata* is restricted to F and the Reno-dunal district (R), whereas *Avenula pubescens* is restricted to these districts and Z. *Agrimonia eupatoria*, *Eryngium campestre* and *Lathyrus tuberosus* are restricted to F, Z, E and R. *Bromus inermis* and *Euphorbia esula* are former fluvial species that are now more widespread.

Rarity of species

All communities except II and IX contained one species classed as being in rarity category 3 (i.e. rare) (see figure 7): *Tragopogon pratensis ssp. orientalis*. The relatively large proportion of species of rarity category 4 (i.e. fairly rare) in the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) was striking. Four species were involved: *Allium oleraceum, Peucedanum carvifolia, Pimpinella major* and *Rumex thyrsiflorus*. Less common (rarity category 5) were: *Avenula pubescens, Bromus inermis, Cichorium intybus, Eryngium campestre, Lathyrus tuberosus, Leontodon hispidus, Medicago falcata, Valerianella locusta* and *Verbena officinalis*.

The *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) had the largest proportion of rare to fairly common species (8.5%), followed by the *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV) and the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) with respectively 4.1% and 3.2%. In the fragmentary community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion*/ *Chenopodion*] (VIII) only common to extremely common species occurred.

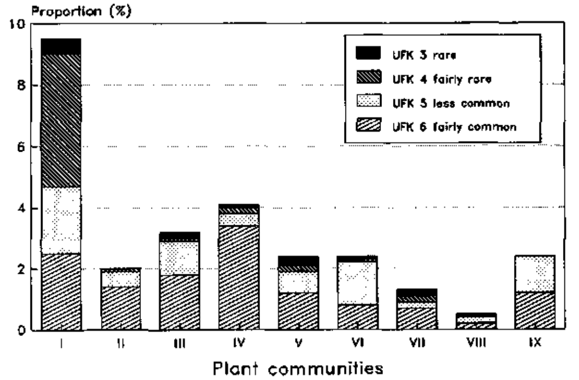


Figure 7. Percentages of the most important national rarity categories in 1980 represented within the plant communities.

Ecological indicator value for soil fertility

The difference between the plant communities in mean indicator value for soil fertility is only slight. It varies from 6.2 to 6.9 (see table 21). The proportion of species indicating nutrient-poor soils (N_{1-4}; i.e. 'poor' species) was relatively high in communities III, IV and VI and extremely low in community IX.

Table 21. Mean indicator value for soil fertility (according to Ellenberg, 1974) and quantification index for nutrient-poor N_{1-4} and nutrient-rich N_{7-9} soils calculated by taking the abundance of the species into account.

Plant comm.	Mean N_{1-9}	Mean abundance N_{1-4}	N_{7-9}	Ratio
I	6.6	5.5	46.5	0.12
II	6.8	6.8	57.5	0.12
III	6.2	10.1	36.6	0.28
IV	6.2	8.4	36.6	0.23
V	6.5	5.1	46.2	0.11
VI	6.2	8.4	38.9	0.22
VII	6.5	4.8	44.4	0.11
VIII	6.6	2.8	49.6	0.06
IX	6.9	0.2	57.5	0.00

3.3.3 Development of the vegetation

Plant communities

Table 22 shows the number of permanent plots assigned to the different plant communities in 1987, 1990, 1992 and 1994. This table also shows the proportions of the plant communities in those four years. The same 209 permanent plots were measured in the four years. The most important changes were the disappearance of the two fragment communities (with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX), and with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII)) and the sharp decline of the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII). The *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) and the *Arrhenatheretum with Urtica dioica* and *Valeriana officinalis* (II) increased sharply.

Table 22. Distribution of the 209 permanent quadrats among the plant communities in 1987, 1990, 1992 and 1994.

Plant community	1987 n	1987 %	1990 n	1990 %	1992 n	1992 %	1994 n	1994 %
I	11	5	16	8	16	8	18	9
II	.	.	12	6	21	10	26	12
III	11	5	27	13	25	12	27	13
IV	9	4	12	6	6	3	2	1
V	10	5	43	21	77	37	90	43
VI	42	20	74	35	54	26	43	21
VII	86	41	25	12	10	5	3	1
VIII	35	17	.	.	.	.	.	.
IX	5	2	.	.	.	.	.	.

Species diversity within the plant communities between 1987 and 1994

Figure 8 shows the species diversity per plant community in the separate years of the study. Species diversity in the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) and in the *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV) increased between 1987 and 1994. By contrast, species diversity in the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) decreased in the same period. The species diversity in the other plant communities decreased between 1987 and 1990 but slightly increased thereafter. The *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) first appeared in 1990.

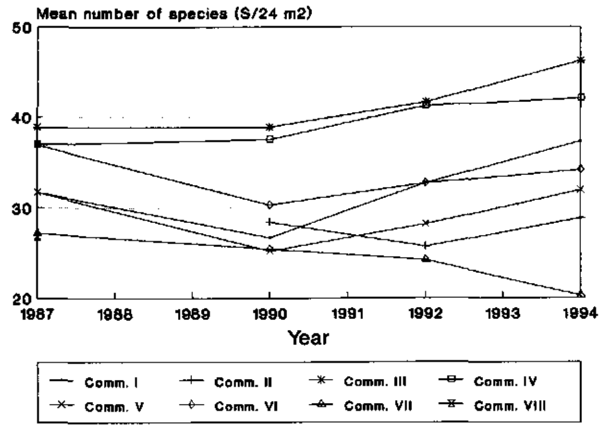


Figure 8. Number of species per plant community in 1987 to 1994.

Table 23 shows the mean number of species per plant community in 1987, 1990, 1992 and 1994. Homogeneous groups are at $p<0.05$ level. With the exception of 1987, the species diversity of communities III and IV was significantly ($p<0.05$) higher than of all other plant communities. In 1994 species diversity of community II was sinificantly lower than of all other communities, except community VII.

Table 23. Mean number of species per plant community in 1987, 1990, 1992 and 1994. Homogeneous groups at p<0.05 level.

1987 Plant comm.	Number of species	Homogeneous groups	1990 Plant comm.	Number of species	Homogeneous groups
III	38.9	a . .			
IV	37.0	a b .	III	38.9	a . .
VI	36.9	a b .	IV	37.5	a . .
IX	34.6	a b .	VI	30.3	. b .
I	31.7	. b c	II	28.4	. b c
V	31.7	. b c	I	26.7	. . c
VII	27.2	. . c	VII	25.4	. . c
VIII	26.8	. . c	V	25.2	. . c

1992 Plant comm.	Number of species	Homogeneous groups	1994 Plant comm.	Number of species	Homogeneous groups
III	41.6	a . . .	III	46.2	a . . . .
IV	41.2	a . . .	IV	42.0	a b . . .
VI	32.7	. b . .	I	37.3	. b . . .
I	32.7	. b . .	VI	34.1	. b c . .
V	28.2	. . c .	V	31.9	. . c . .
II	25.7	. . c d	II	28.8	. . . d .
VII	24.2	. . . d	VII	20.3	. . . . e

Succession between 1987 and 1994

Table 24 shows the change in vegetation composition by the number of permanent plots that changed community or were the same in 1987 and in 1994. It should be noted that community II was not found in 1987. %-PC is the proportion of the total number of permanent plots of a community of 1987 which had developed in a certain direction by 1994. When two communities are connected by an arrow, it does not mean that one arose directly from the other, since intermediate communities may have occurred during the years that are not considered in the table. Table 24 shows that 31 permanent plots did not change community in the eight years after dike reconstruction. All these permanent plots belonged to one of the communities of the *Arrhenatheretum* (communities I to VII). Three permanent plots of the fragment community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) developed into the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V), whereas 1 plot belonged to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) in 1994 and 1 plot to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). One permanent plot of the fragment community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) developed into the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I), i.e. the direction of the best developed *Arrhenatheretum* vegetation. Most of the permanent plots (69%) of the fragment community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) developed into the *Arrhenatheretum* with dominance of

Table 24. Changes in vegetation composition between 1987 and 1994.

Shift 1987	→	1994	N	%-PC
I	→	I	11	100
III	→	II	8	73
III	→	III	3	27
IV	→	II	3	33
IV	→	III	4	44
IV	→	V	2	22
V	→	III	6	60
V	→	V	3	30
V	→	VI	1	10
VI	→	II	2	4
VI	→	III	1	2
VI	→	V	28	67
VI	→	VI	11	26
VII	→	I	6	7
VII	→	II	13	15
VII	→	III	12	14
VII	→	IV	2	2
VII	→	V	30	35
VII	→	VI	20	23
VII	→	VII	3	4
VIII	→	I	1	3
VIII	→	V	24	69
VIII	→	VI	10	29
IX	→	III	1	20
IX	→	V	3	60
IX	→	VI	1	20
total			209	

Alopecurus pratensis (V) whereas 10 plots were classified as *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) in 1994. All permanent plots assigned to the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) in 1987 were still in that community in 1994.

Changes in vegetation composition between 1987, 1990, 1992 and 1994
From 1987 to 1994 all permanent plots were assigned to one of the plant communities distinguished. Successional changes in species composition were responsible for shifts from one community to another. A succession scheme was prepared by grouping these shifts and indicating major and minor succession lines (see figure 9 and 10).

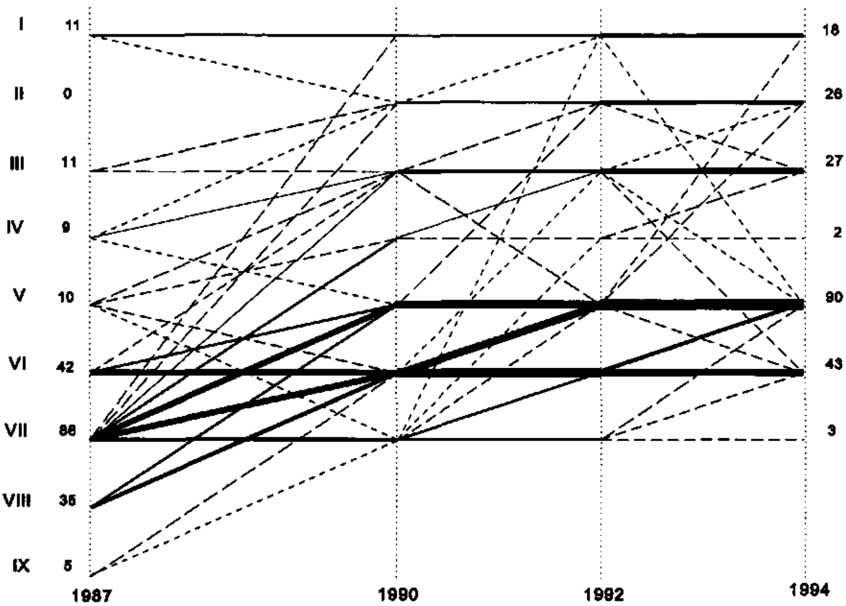


Figure 9. Succession scheme of period 1987-1994 and number of permanent plots in 1987 and 1994. The line thickness increases with the frequency of shifts.

The developmental tendencies in the vegetation are clearly indicated by the divergence and convergence of the succession lines. Divergent lines indicate a decrease in the number of permanent plots of a community, convergent lines an increase. The scheme shows the direction of the changes that occurred after the reconstruction. Both progressive and retrogressive succession took place, the latter probably caused by negative effects of some management regimes applied.

The succession scheme can also be approached in terms of systems theory, with the entire experimental dike considered as an ecosystem. For any given year, the system consists of a number of communities which are subject to change. A series of changes within a system is a transformation (Ashby, 1964; Van der Maarel, 1966). Figure 10 shows the transformations observed between 1987, 1990, 1992 and 1994.

From 1987 to 1994 the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) increased very slowly from 11 to 18 plots. This optimally developed plant community, which was characteristic of the spared zone, only developed in some plots directly bordering the spared zone and was probably able to do so because of the rain of seeds from the spared zone. Six permanent plots developed directly from the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) to the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I), one permanent plot developed directly from the fragment community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) to community I.

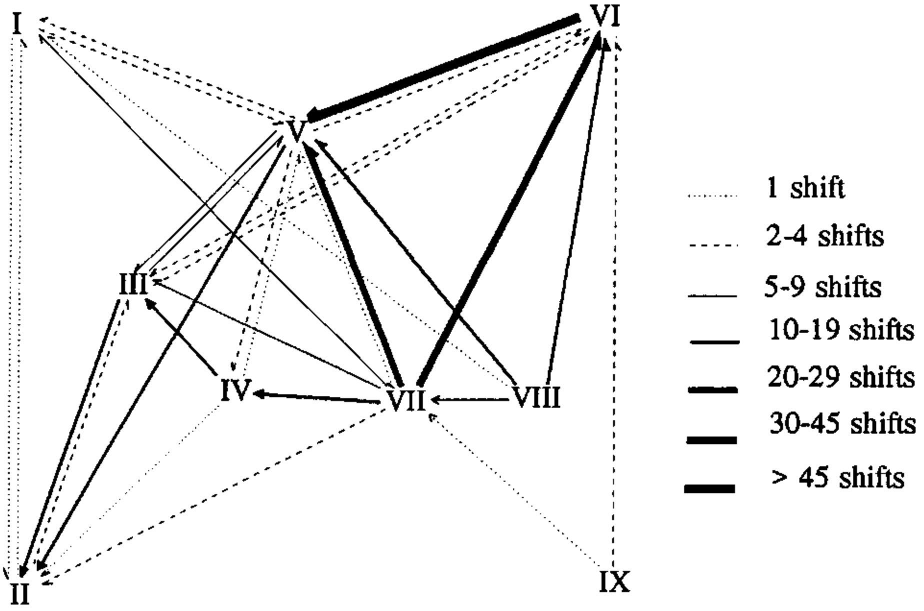


Figure 10. Succession scheme as a kinematic graph. The arrow thickness increases with the frequency of the shifts.

The *Arrhenatheretum with Urtica dioica* and *Valeriana officinalis* (II) developed after 1987 and increased steadily, occurring in 26 plots by 1994. This community is considered to be a degraded stage caused by bad management regimes. The *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) increased quickly from 1987 to 1990, after which it remained steady. Since community III is considered to be the second best developed vegetation after community I, arrows pointing towards community III can be expected to indicate progressive developments and arrows pointing away from community III retrogressive developments. The *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV) showed a very slight increase to 1990 but decreased sharply from 12 (1990) to 2 plots in 1994. The *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) showed a strong increasing trend from 10 plots in 1987 to 90 plots in 1994. It mainly devoloped out of the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII). Community V is intermediate between communities III and VI. Under hay-making regimes it will probably develop into community III, under grazing regimes to community VI. The *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) almost doubled from 42 to 74 plots in 1990 after which it gradually decreased to 43 plots in 1994. The increase was mainly due to relevés originating from the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) and from the fragment community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII). The decrease after 1990 was mainly caused by transformation of plots to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). Under a grazing regime, community VI will probably develop further into a real pasture vegetation. The association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) almost disappeared after a strong decrease from 86 plots in 1987 to only 3 plots in 1994. The pioneer communities with a considerable *Eu-Polygono-Chenopodion* element disappeared completely after 1987.

The succession was from the fragment community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) and the fragment community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) via the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) to the central community: the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). From community V the succession was to all other communities, except communities VIII and IX. In general the dike vegetation did strongly converge into the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V), which is of low botanical value. Fortunately, the number of plots with communities of greater botanical value (i.e. I and III) increased concomitantly at the same time from 22 to 45.

Ordination diagram

The eigenvalues of the first four ordination axes were respectively 0.431, 0.087, 0.015 and 0.003. Only the first two axes were used for the explanation of the variation in the data. These two dimensions account for an extracted variance of 52%. Figure 11 shows the ordination diagram of axis 2 against axis 1.

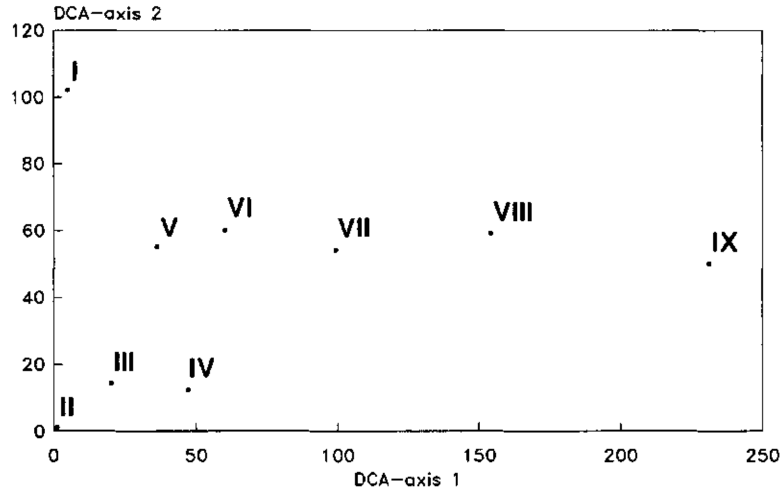


Figure 11. Ordination diagram of axis 2 against axis 1.

Table 25 shows the correlation between the axes of the Detrended Correspondence Analysis and the syntaxonomical elements. Decorana axis 1 appeared to be positively correlated with the *Chenopodietea* and the *Plantaginetea* (respectively $p < 0.001$ and $p < 0.01$) and negatively correlated with the *Arrhenatheretum* and the *Molinio-Arrhenatheretea* (respectively $p < 0.001$ and $p < 0.01$). Respectively 88% and 58% of the variation along the first axis of the ordination diagram was explained by a decrease in characteristic species of the *Arrhenathereum elatioris* and the *Molinio-Arrhenatheretea* and respectively 86% and 64% was explained by an increase in species of the *Chenopodietea* and the *Plantaginetea*. Although not significant, the *Artemisietea* show a rather high negative correlation with the first axis. Additionally, there appeared to be a significantly ($p < 0.001$) negative correlation (r - 0.5673) between DCA-axis 1 of the ordination of the 808 separate relevés and their age. This clearly indicates the expansion of perennials at the expense of annuals between 1987 and 1994. Decorana axis 2 was positively correlated with the *Koelerio-Corynephoretea* together with the *Festuco-Brometea*, though not statistically significantly. Only 28% of the variation along the second axis of the ordination diagram was explained by an increase in species of dry grasslands belonging to the *Koelerio-Corynephoretea* together with the *Festuco-Brometea*. From this it could be concluded that the degree of development of the plant communities distinguished was shown along the horizontal axis, ordination axis 1. The least developed plant communities were situated on the right-hand side of the ordination diagram whereas the most developed succession stages were situated on the left-hand side.

Table 25. Pearson correlation coefficients (r) and coefficients of determination (r^2 in %) between axes of Detrended Correspondence Analysis and syntaxonomical elements.

Syntaxonomical elements	DCA axis 1		DCA axis 2	
	r	r^2	r	r^2
Molinio-Arrhenatheretea	-0.76*	58%	-0.34	12%
Arrhenatheretum	-0.94**	88	-0.04	0
Lolio-Cynosuretum	-0.10	1	0.28	8
Koel.Coryn.& Fest.Brom.	-0.25	6	0.53	28
Trifolion medii	-0.59	35	-0.15	2
Artemisietea	-0.70	49	-0.24	6
Plantaginetea	0.80*	64	0.20	4
Chenopodietea	0.93**	86	0.09	1

n of cases: 9; 1-tailed signif: *: p<0.01, **: p<0.001

Indicative species

Table 26 shows the correlation between the axes of the Detrended Correspondence Analysis (DCA) and the proportion of species indicative of nitrogen-poor and nitrogen-rich conditions, of pastures and hay meadows. The correlation between the DCA axes and the mean number of species in the communities is also given.

Decorana axis 1 appeared to be positively correlated to the species indicative of pastures ($p<0.01$) and negatively with the species indicative of hay meadows and species characteristic of nitrogen-poor conditions (respectively $p<0.001$ and $p<0.01$). The explanation variables for the variation along the first axis of the ordination diagram were an increase in pasture species (62%) and decreases in hay meadow species (86%) and in species of nitrogen-poor conditions (64%). There was no statistically significant correlation between the species richness of the plant communities and the DCA axes.

Table 26. Pearson correlation coefficients (r) and coefficients of determination (r^2 in %) between DCA axes and indicative species for respectively nitrogen-poor N_{1-4} and nitrogen-rich N_{7-9} conditions, pastures, hay meadows and species richness of the plant communities.

Indicative species	DCA axis 1		DCA axis 2	
	r	r2	r	r2
Nitrogen-poor species	-0.80*	64%	-0.43	19%
Nitrogen-rich species	0.41	17	0.05	0
Pasture species	0.79*	62	0.21	4
Hay meadow species	-0.93**	86	-0.26	7
Species richness	-0.14	2	-0.35	12

n of cases: 9; *: p<0.01, **: p<0.001

3.3.4 Comparison of the flora before and after the reconstruction

Altogether, in all years 196 plant species were found on the experimental dike; 36 of them were grasses and grass-like species, 160 were herbs. In the 1978 inventory the grasses and grassy species were omitted, so only the number of herbs could be compared before and after the reconstruction.

As compared with 1978, by 1994 only 2 of the herb species that had been present in 1978 had not reappeared on the experimental dike (see figure 12): *Knautia arvensis* and *Viola odorata*. This means that about 98% of all herb species found in 1978 reappeared in the first eight years after the reconstruction. Of the reappeared species, one disappeared after 1987 and two after 1990. 83 species were found in all years of the research. In the period 1987-1994 72 species appeared which were not found in 1978 (see figure 12). Many of them were indeed new species, but others had not been recognized or had been overlooked in 1978. By 1994 only 37 of these new species remained.

Frequency of species was also used for the comparison. Here, frequency means the proportion of sample plots in which species were found. On the basis of frequency of the species before and after the reconstruction, three main categories of species were distinguished; within these categories the following minor groups were distinguished:

1. Species present before the reconstruction and that did not reappear: *Knautia arvensis* and *Viola odorata*.

2. Species present before and after the reconstruction:
   - a Sharp increase (>5%) followed by a further increase after 1987: *Cirsium arvense, Geranium dissectum, Lathyrus pratensis, Leucanthemum vulgare, Symphytum officinale, Trifolium pratense, Vicia cracca, Vicia sepium,*
   - b Sharp increase (>5%) to 1987 and remaining steady thereafter: *Cerastium fontanum, Medicago lupulina,*
   - c Sharp increase (>5%) to 1987 followed by a decrease: *Capsella bursa-pastoris, Carduus crispus, Plantago lanceolata, Polygonum persicaria, Ranunculus repens, Sinapis arvensis, Stellaria media, Taraxacum officinale, Trifolium repens,*
   - d About equal but increasing after 1987: *Allium vineale, Bellis perennis, Euphorbia esula, Ranunculus acris, Tanacetum vulgare, Trifolium dubium, Vicia sativa ssp. nigra,*
   - e About equal and remaining steady after 1987: *Galium aparine, Pulicaria dysenterica, Senecio erucifolius, Verbena officinalis,*
   - f About equal but decreasing after 1987: *Angelica sylvestris, Arctium pubens, Artemisia vulgaris, Calystegia sepium, Cirsium vulgare, Geranium molle, Leontodon hispidus, Potentilla anserina,*
   - g Sharp decrease (>5%) to 1987 followed by an increase: *Anthriscus sylvestris, Centaurea jacea, Crepis biennis, Daucus carota, Galium mollugo, Glechoma hederacea, Heracleum sphondylium, Lamium album, Lysimachia nummularia, Plantago media, Potentilla reptans, Prunella vulgaris, Ranunculus bulbosus, Rumex acetosa, Senecio jacobea, Tragopogon pratensis ssp. orientalis, Veronica chamaedrys,*

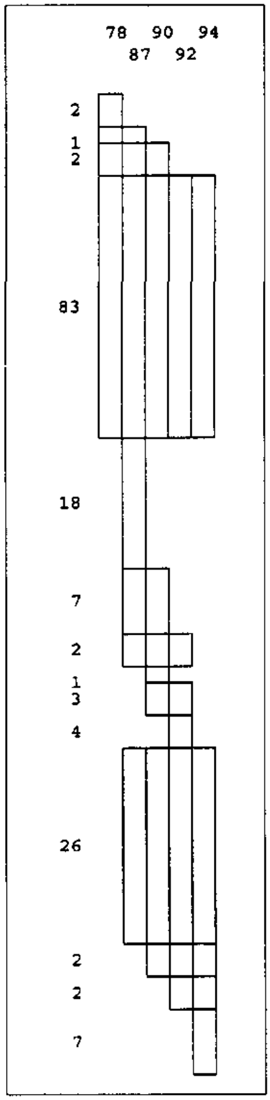


Figure 12. Presence of herb species in 1978, 1987, 1990, 1992 and 1994. The numbers indicate the number of species found.

h Sharp decrease (>5%) to 1987 and remaining steady thereafter: *Achillea millefolium, Agrimonia eupatoria, Allium oleraceum, Campanula rotundifolia, Cerastium arvense, Cichorium intybus, Convolvulus arvensis, Cruciata laevipes, Equisetum arvense, Filipendula ulmaria, Lathyrus tuberosus, Linaria vulgaris, Lotus corniculatus, Ononis repens ssp. spinosa, Ornithogalum umbellatum, Pastinaca sativa, Peucedanum carvifolia, Pimpinella major, Rosa canina, Rubus caesius, Rumex thyrsiflorus, Stachys palustris, Urtica dioica, Valeriana officinalis, Valerianella locusta, Verbascum nigrum,*

i Sharp decrease (>5%) followed by a further decrease: *Epilobium hirsutum, Melilotus altissima, Papaver rhoeas, Polygonum amphibium, Trifolium campestre.*

3. Species absent before the reconstruction:

a Sharp increase (>5%) to 1987 followed by a decrease: *Carduus nutans, Chenopodium album, Erigeron canadensis, Matricaria maritima, Matricaria recutita, Plantago major, Polygonum aviculare, Rorippa sylvestris, Senecio vulgaris, Sonchus asper, Sonchus oleraceus,*

b Sharp increase (>5%) to 1987 and remaining steady thereafter: *Rumex crispus, Rumex obtusifolius,*

c Sharp increase (>5%) to 1987, continuing more strongly thereafter: *Crepis capillaris, Trifolium hybridum,*

d Small increase (<6%) to 1987 and remaining steady thereafter or followed by a decrease and/or disappearance after 1987: 57 species.

Table 27. Frequency of change (increase, staying equal and decrease) of species in periods 1978-1987 (including reconstruction), 1987-1994 and 1978-1994. Only species occurring in 1978 are considered.

			1987-1994					
1978-1987	N	(%)	Increase	Equal	Decrease	1978-1994	N	(%)
Increase	19	(22)	8	2	9	Increase	23	(26)
Equal	19	(22)	7	4	8	Equal	18	(21)
Decrease	50	(56)	17	28	5	Decrease	47	(53)
Total	88		32	34	22	Total	88	

Immediately after the reconstruction the frequency of 50 of 88 species had decreased (56%), whereas the frequency of 19 species increased (22%) (see table 27). Between 1987 and 1994 the frequency of 17 of 50 species that decreased from 1978 increased, whereas the frequency of 9 of 19 species that increased from 1978 decreased. In 1994 the frequency of 47 of 88 species (53%) was still lower than before the reconstruction, and of 23 species (26%) it had increased even more since the reconstruction. In 1994 the frequency of 18 species (21%) was the same as before the reconstruction (21%).

A few species appeared only in the spared zone in 1987: *Calamagrostis epigejos, Peucedanum carvifolia, Rumex thyrsiflorus* and *Verbascum nigrum*. After three years they also appeared in trial plots where no zone was spared. As all of these plots directly bordered the spared zone it seems probable that the species involved dispersed from that zone.

3.4 DISCUSSION

3.4.1 Plant communities

In the period 1987-1994, directly after a large-scale reconstruction, 9 plant communities were distinguished on the experimental dike. In 1994, at the end of the study, only 5 communities remained to an important degree, 2 communities had almost disappeared and 2 communities had already disappeared by 1990.

Both frequency and mean abundance of the characteristic species of the *Arrhenatheretum* showed that community I, the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus*, was the most saturated *Arrhenatheretum elatioris* vegetation of all communities. This means that in community I the most characteristic species of the *Arrhenatheretum* were found. On the basis of differential species of subassociation group B and especially the subassociation *picridetosum*, community I was considered as the only community belonging to subassociation group B of the *Arrhenatheretum* and it might be designated to the *picridetosum* subassociation. A sowing experiment with *Picris hieracioides* in the intact vegetation showed that the absence of this characteristic species was probably due to failure of dispersion and not to failed germination and establishment (see also Chapter 8). The species diversity of community I was intermediate, caused by the absence of proper management during the reconstruction. Lack of appropriate management also caused an increase of species assigned to the *Artemisietea*. After the reconstruction the species diversity increased from 27 species in 1990 to 37 species in 1994. This community had the largest proportion of rare to fairly common species (8.5%), with an especially large proportion of species of rarity category 4 (i.e. fairly rare). Community I was almost exclusive the spared zone (see Chapter 4). Compared with the overview of plant communities given by Van der Zee (1992) community I most resembled the *Arrhenatheretum*, transition community of *Origanum vulgare* and *Euphorbia esula* [subass. group A/subass. group B]. This community is very rare on the dikes of the river Waal and is considered to be of great interest for nature conservation. It has been singled out for its botanical interest by many authors (Cohen Stuart & Westhoff, 1963; Neijenhuis, 1968, 1969; Sýkora & Liebrand, 1986, 1987; Van der Steeg, 1988; Van der Zee, 1992).

Although community II, the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis*, contained a relatively large proportion of the *Artemisietea*, it was still assigned to the *Arrhenatheretum elatioris* because of the proportions of the characteristic species of this association in this community. The species diversity was low, mostly because of the low number of herbs. Community II showed the greatest species resemblance (72%) to the fragmentary community of *Alopecurus pratensis* and *Heracleum sphondylium* [*Arrhenatherion*/*Artemisietea*] as distinguished by Van der Zee (1992). In general, this community was found in permanent plots with inappropriate management regimes (see Chapters 4 and 5). If this inappropriate management, which mainly consists of mowing without removing the mowings, is continued long enough, the tall nitrofilous species like *Urtica dioica*, *Galium aparine* increase further and community II shifts towards the *Artemisietea* (Van der Zee, 1992).

In plant communities III to VI the proportion of characteristic species of the *Arrhenatheretum elatioris* was nearly the same. However, as the overall floristic composition differed, a subdivision was possible. Community III, the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia*, showed the greatest resemblance (73%) to the *Arrhenatheretum* subass. group A, variant with *Potentilla reptans* and *Galium mollugo* as distinguished by Van der Zee (1992) but also a great resemblance (68%) to the *Arrhenatheretum* subass. group B, *brizetosum*, variant with *Galium verum* and *Pimpinella saxifraga*. It seems possible that community III will further develop towards the latter community in the future. The management regime will play an important role in this process. Throughout the study period the species diversity of community III was the greatest; this community contained the highest number of herbs and the highest number of grasses. Furthermore, it increased from 39 species in 1987 to 46 in 1994. In 1994 the proportion of rare to fairly common species was already 3.2%. The species diversity will probably further increase in the future. In general, this community was found in permanent plots with correct management practices, especially hay-making regimes (see Chapters 4 and 5). If the management regime changes adversely, the species diversity will dwindle rapidly and community III will consequently shift to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) and in a later stage even to the *Artemisietea*.

Community V, the *Arrhenatheretum* with dominance of *Alopecurus pratensis*, showed the greatest resemblance (69%) to the *Arrhenatheretum* subass. group A, variant with *Potentilla reptans* and *Galium mollugo* as distinguished by Van der Zee (1992). Further development from this 'central' community towards hayland communities or meadow communities will follow, depending on the management regime applied. The relatively low species diversity was probably caused by the dominance of the tall grass species *Alopecurus pratensis*. Between 1990 and 1994 the diversity increased. A shift towards community III or community VI (depending on whether the management involves hay-making or grazing) is anticipated.

Community VI, the *Arrhenatheretum/Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens*, contained many characteristic species of the *Arrhenatheretum elatioris* and of the *Lolio-Cynosuretum*. Therefore it was considered to be a transition between these associations. This was confirmed by the great overlap in species (70%) with the *Lolio-Cynosuretum* subassociation *ononidetosum* as distinguished by Van der Zee (1992), although community VI most closely resembled (71%) the *Arrhenatheretum* subass. group A, variant with *Potentilla reptans* and *Galium mollugo*, as distinguished by Van der Zee. Under grazing management community VI will probably develop into a real meadow community. The species of the *Arrhenatheretum* will dwindle gradually but the species of the *Lolio-Cynosuretum* will increase. At present this community is less developed because pasture communities develop more slowly than hay meadow communities. This is because species in intensively grazed pastures are hardly able to flower and make seeds. In contrast, in hay meadows there is an annual seed rain of almost all species, which promotes rapid increase in the numbers of the various species. The species diversity of community VI was intermediate. Between 1990 and 1994 it increased from 30 to 34 species. Immediately after the reconstruction it was found under various management regimes. In 1994 however it was mainly found in grazed permanent plots and in some plots with hay-making in combination with grazing (see Chapter 5).

In 1994 communities IV and VII had almost disappeared. Community IV, the *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense*, showed the highest species resemblance (64%) with the fragmentary community of *Alopecurus pratensis* and *Heracleum sphondylium* [*Arrhenatherion/Artemisietea*] as distinguished by Van der Zee (1992) but also a high resemblance with the *Arrhenatheretum* subass. group A, variant with *Potentilla reptans* and *Galium mollugo* (63%) and with the *Lolio-Cynosuretum* subassociation *ononidetosum* (62%). The species diversity of community IV was second highest of all communities distinguished, because of the relatively high number of herbs. This community initially consisted of a mixture of several syntaxonomic species groups, many of which declined sharply during the years. The management caused a shift towards a hay meadow community or towards a pasture community. By 1994 community IV had almost disappeared.

Plant community VII lacked many of the characteristic species of the *Arrhenatheretum elatioris*, but nevertheless could be assigned to this association on the basis of the presence of a few characteristic species. Because of this incompleteness community VII was considered to be an association fragment of the *Arrhenatheretum elatioris* (Kopecky & Hejny, 1974; Schaminée *et al.*, 1990). The establishment of new species caused a shift to all the other plant communities, except VIII and IX; in 1994 community VII had almost disappeared.

In 1990 communities VIII and IX had already disappeared. Plant community VIII, a fragmentary community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion elatioris/Eu-Polygono-Chenopodion*], contained only 4 characteristic species of the *Arrhenatheretum elatioris* which besides had low abundance. In contrast, the proportion of characteristic species of the *Chenopodietea* was high, especially of the sub-alliance *Eu-Polygono-Chenopodion*. Community VIII was therefore considered to be a transition between the *Eu-Polygono-Chenopodion* and the *Arrhenatherion*. This community representing an early successional stage had already disappeared in 1989.

Community IX, a fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*], contained only 2 characteristic species of the *Arrhenatheretum elatioris*: *Arrhenatherum elatius* and *Galium mollugo*. Because of the high proportion of characteristic species of the alliance *Polygono-Chenopodion* and especially of the sub-alliance *Eu-Polygono-Chenopodion*, community IX was considered to be a fragment of the sub-alliance *Eu-Polygono-Chenopodion*. Although communities VIII and IX both showed the greatest species resemblance to the *Lolio-Plantaginetum* as distinguished by Van der Zee (1992), this resemblance was not enough to justify assigning these communities to that association. The phytosociological composition of the fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) was very different from the other plant communities; the proportion of species of the *Molinio-Arrhenatheretea* and of the *Artemisietea* was relatively small whereas the proportions of the *Plantaginetea* and of annual pioneer species of the *Chenopodietea* and the *Secalietea* were relatively large. The species diversity was relatively high, thanks to the many annual pioneer species occurring immediately after the reconstruction. This community representing the earliest successional stage had already disappeared in 1988.

Adjustment to the review of Schaminée et al. (1996, 1998)
On the basis of differential species of subassociation group B of the *Arrhenatheretum elatioris* (Westhoff & Den Held, 1969) and especially the subassociation *picridetosum*, community I, the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus*, was considered as the only community belonging to subassociation group B of the *Arrhenatheretum* and it might be designated to the *picridetosum* subassociation. According to the review of Schaminée *et al.* (1996) community I might be designated to the *Arrhenatheretum festucetosum arundinaceae*.

In spite of the presence of a number of differential species of sub-association group B of the *Arrhenatheretum elatioris*, the species which are differential of sub-association group A dominated in community II to VIII. Because the species of sub-association group B occurred only sporadically and with low abundance in communities II to VIII, these communities were retained in sub-association - group A. Nearly all species differential of the *alopecuretosum* sub-association were found. However, almost all of them had a low abundance and therefore this vegetation could be assigned to the *inops* sub-association. According to the review of Schaminée *et al.* (1996) community II to V might be designated to the *Arrhenatheretum typicum*.

Although community II, the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis*, contained a relatively large proportion of the *Artemisietea*, it was still assigned to the *Arrhenatheretum elatioris* because of the proportions of the characteristic species of this association in this community. Community II showed the greatest species resemblance (72%) to the fragmentary community of *Alopecurus pratensis* and *Heracleum sphondylium* [*Arrhenatherion/Artemisietea*] as distinguished by Van der Zee (1992). In general, this community was found in permanent plots with inappropriate management regimes (see Chapters 4 and 5). If this inappropriate management, which mainly consists of mowing without removing the mowings, is continued long enough, the tall nitrofilous species like *Urtica dioica*, *Galium aparine* increase further and community II shifts towards the *Artemisietea* (Van der Zee, 1992). In terms of the review of Schaminée *et al.* (1996) community II might develop to the *Tanaceto-Artemisietum typicum*.

Community III, the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia*, showed the greatest resemblance (73%) to the *Arrhenatheretum* subass. group A, variant with *Potentilla reptans* and *Galium mollugo* as distinguished by Van der Zee (1992) but also a great resemblance (68%) to the *Arrhenatheretum* subass. group B, *brizetosum*, variant with *Galium verum* and *Pimpinella saxifraga*. It might be possible that community III will further develop towards the latter community in the future. According to the review of Schaminée *et al.* (1996) community III might develop to the *Arrhenatheretum medicaginetosum falcatae*.

Because of a relatively low proportion of *Arrhenatheretum* species and relatively high proportions of *Lolio-Cynosuretum* and *Plantaginetea* species community VI is assigned as a transition between *Arrhenatheretum* and *Lolio-Cynosuretum*. To distinguish this community from the other

Arrhenatheretum communities it henceforth is called a *Lolio-Cynosuretum* community: *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI). In terms of the review of Schaminée *et al.* (1996) community VI might be designated to the *Lolio-Cynosuretum typicum*.

A lack of character species made it difficult to assign communities VII and VIII at the association level. However, the species that were present made inclusion of community VII in the *Arrhenetheretum* association justifiable. It was assigned as an association fragment. According to the review of Schaminée *et al.* (1996) community VII might be assigned as an association fragment of the *Arrhenatheretum typicum*. Community VIII was determined as a transition between the *Eu-Polygono-Chenopodion* and the *Arrhenatherion elatioris*. Community IX is assigned as an fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*]. In accordance to the review of Schaminée *et al.* (1998) community IX might be designated to the trunk community RG *Matricaria recutita-Papaver rhoeas*-[*Papaveretalia rhoeadis*]. Therefore, community VIII might be assigned as an transition between the RG *Matricaria recutita-Papaver rhoeas*-[*Papaveretalia rhoeadis*] and the *Arrhenatherion elatioris*.

Nature conservation interest of the plant communities on the reconstructed dike
In the Netherlands the so-called stream valley plants are restricted to the fluviatile district and one or two other districts and therefore many are rare. In this study 17 fluvial species were found on the experimental dike. Two of them, *Peucedanum carvifolia* and *Rumex thyrsiflorus*, only occurred in the spared zone immediately after the reconstruction. After 1987 they dispersed to bordering parts of the dike. The other species were also found in the replaced sods and on the replaced topsoil.

One rare species, four fairly rare species and nine less common were found. The *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) was the most valuable community because of the relatively large proportion of rare to fairly common species (8.5%). As community I mainly occurred in the spared zone (see Chapter 4) it cannot be said that this high proportion of rare to fairly common species is due to regeneration. The *Arrhenatheretum elatioris* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) was also a valuable community because of the high species diversity and the relatively large proportion of rare to fairly common species (3.2%). This proportion was attributable to regeneration. The *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) was less valuable in 1994, but might become more valuable if the species diversity increases. The *Arrhenatheretum elatioris* with dominance of *Alopecurus pratensis* (V) was of relatively low value. Only under correct management regimes it can be expected that the species diversity and the botanical value will increase. The species diversity and the proportion of rare to fairly common species of the *Arrhenatheretum elatioris* with *Urtica dioica* and *Valeriana officinalis* (II) was very low. This community was almost restricted to inappropriate management regimes. If the management regimes are not improved, the botanical value will stay at its present low level or may even further decrease. The other communities (i.e. IV, VII, VIII, XI) had (almost) disappeared in 1994.

3.4.2 Development of the vegetation between 1987 and 1994

The fragmentary community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) and the fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) had already disappeared in the first years of the experiment. The closing of the vegetation cover caused a sharp fall in the annual pioneer species characteristic of the *Chenopodietea*. These therophytes cannot withstand competition from perennial grasses and herbs from later successional stages (Down, 1973; in Kent & Coker, 1992). The expansion of perennials at the expense of annuals is confirmed by the ordination diagrams in which the first axis is clearly related to a decrease of *Chenopodietea* and *Plantaginetea* species in combination with an increase of syntaxonomic elements of plant communities mainly consisting of perennials, in particular *Molinio-Arrhenatheretea*, *Artemisietea* and *Trifolio medii*. These results are in accordance with the finding of Zwaenepoel (1995) that a switch from annual to perennial vegetation in newly sown verges mainly occurred within three years. Between 1987 and 1990 the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) appeared at first, but only on the replaced sods and on replaced topsoil (see Chapter 4). In this case the former species-rich sods within 3 years showed an undesirable change to a more species-poor vegetation with tall forbs. The majority of the relevés composing community II in 1990 were derived from the more species-rich communities I, III and IV. Community II increased steadily from 1990 to 1994 by ruderalization of plots from more species-rich communities. The most species-rich community the *Arrhenatheretum elatioris* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) increased in the first period of the research, developing from various source communities. Although minor shifts occurred into and from other communities, the number of plots of this community remained the same from 1990 to 1994. The *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV), the second most species-rich community, slightly increased in the first years, mainly developing from the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII). This positive trend continued in later years by plots developing into the *Arrhenatheretum elatioris* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). In the first period of the experiment the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) increased sharply, largely because of a shift of plots from the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII), the very species-poor pioneer grassland. The species richness of community V is only moderate. In later years the increase continued, resulting in the preponderance of community V on the dike in 1994. That increase was mainly due to shifts from the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI), which means a decrease in species diversity. The *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) increased sharply at first, because of shifts of relevés from the pioneer communities VII and VIII; it subsequently decreased by losing plots to community V. In 1994 the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) was still the second most frequent vegetation type. Although the pioneer grassland the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) was initially the most frequent, it had almost disappeared by the end. Plots changed into all other communities except the annual communities VIII and IX. The main thrust of change, however, was into the communities V and VI, the *Arrhenatheretum* with dominance of *Alopecurus pratensis* and the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens*. The proportion of the best developed plant community with the highest botanical value, the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I), increased only slightly from 1987 to 1994. In the first years after the reconstruction, community I was only recorded on the spared zone. A limited number of plots from the pioneer grassland the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) and from the nitrophilous tall herb grassland the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) changed into this community. These plots directly bordered the spared zone. This indicates the importance of the presence of a species-rich vegetation as a source of plant seeds. The proportion of permanent plots in which there was insufficient change in the vegetation composition to change community rose from 29% in the period 1987-1990 to 67% in 1990-1992 and to 78% in 1992-1994. This indicates that changes in vegetation - caused by succession - mainly occur immediately after a reconstruction and that after a few years changes happen much more slowly. In 1994, at the end of the experiment, only the communities I, II, III, V and IV still occurred frequently, and communities IV and VII had almost disappeared.

Succession trends

Both positive and negative changes took place, the latter probably caused by the negative effects of some management regimes applied. Community I, which was characteristic of the spared zone, was hardly achieved during the study period except in some plots directly bordering the spared zone which probably benefited from the seed rain from that zone. Since community III is considered to be the second best developed vegetation (after community I), arrows pointing towards community III are considered to be positive developments and arrows pointing away from community III negative developments. Community II is considered to be a degraded stage, mainly caused by inappropriate management regimes (see Chapter 4). In view of development towards species-rich communities, arrows pointing towards community II indicate negative developments and arrows pointing away from community II indicate positive developments. Community V is intermediate between communities III and VI. Under hay-making regimes it will probably develop into community III, under grazing regimes into community VI. Additionally, community VI will probably develop further into a real pasture vegetation assigned to the *Lolio-Cynosuretum.*

Each community can be said to show a specific succession-line-characteristic (Londo, 1974). The major succession trend on the experimental river dike was from the fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) and the fragmentary community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) via the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) to the central community, the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). The succession trends were presented in ordination diagrams. The main differentiating factors were determined by interpreting the ordination axes. Respectively 88% and 58% of the variation along ordination axis 1 was explained by a decrease in characteristic species of the *Arrhenatheretum* and the *Molinio-Arrhenatheretea* and respectively 86% and 64% of the variation was explained by an increase in species of the *Plantaginetea* and the *Chenopodietea*. Consequently, the proportion of the *Molinio-Arrhenatheretea* and *Arrhenatheretum* species was negatively correlated with the proportions of the *Plantaginetea* and the *Chenopodietea.* Decorana axis 2 was positively correlated with the *Koelerio-Corynephoretea* together with the *Festuco-Brometea*, though not statistically significantly. Only 28% of the variation along the second axis of the ordination diagram was explained by an increase in species of dry grasslands belonging to the *Koelerio-Corynephoretea* together with the *Festuco-Brometea.* The explanatory variables for the variation along the first axis of the ordination diagram were also an increase in pasture species (62%) and decreases in hay meadow species (86%) and in species of nitrogen-poor conditions (64%). There was no statistically significant correlation between the species diversity of the plant communities and the DCA axes. It can be concluded that the degree of development of the plant communities distinguished is shown along ordination axis 1. The least developed plant communities with species characteristic of pastures and nutrient-rich conditions were situated on the right-hand side of the ordination diagram. The best developed succession stages were situated on the left-hand side. They consisted of hayfields and hay meadows with species characteristic of relatively nutrient-poor conditions. In the left-upper corner the best developed vegetation was located, in which the highest proportion of species characteristic of nutrient-poor, dry grasslands was found.

Although a relatively high species diversity was reached and a number of rare to fairly common species occurred between 1987 and 1994, the succession of the vegetation of recently reconstructed river dikes to species-rich, well developed, relatively stable grasslands containing many rare species will probably take several more years (Oomes, 1988; 1992; Bakker, 1989). Gibson and Brown (1992) even assume that under a grazing regime secondary succession towards species-rich calcicoluos grassland will take at least a century to run its course. In general, immediately after a reconstruction a pioneer vegetation appears, mainly consisting of annual and biennial species found on fields with root and tuber crops and species of disturbed, ruderal stands. Most soils contain seeds of these species, often in state of dormancy. After each disturbance of the soil some of these seeds germinate and these species become dominant for a short period, maintaining their dominance for as long as the vegetation remains quite open. Once the vegetation closes, they disappear as a result of competition. Disturbing the soil also gives seeds of more persistent species, characteristic of instable habitat conditions, the chance to germinate. These mostly biennial and sometimes perennial ruderal species are able to survive for a longer time than the annual pioneer species, only disappearing gradually after a longer period of management directed to the development of a stable grassland. More and more true grassland species establish until at last only the species best adapted to the applied management regime remain. On newly sown verges Zwaenepoel (1995) found a quantative proportion of 68% of spontaneously settled species in the first year, which had decreased to 42% by the third year, the year in which sown grasses became more important than the spontaneous species.

Under different abiotic conditions, for example differences in slope, aspect or soil conditions, different succession trends will operate. It is still too early to predict the vegetation composition on the experimental river dike after stabilization. On the basis of the similarities between the plant communities distinguished by Van der Zee (1992) and the best developed community on the experimental dike, it can be predicted that ultimately the *Arrhenatheretum* subassociation *brizetosum*, variant with *Galium verum* and *Pimpinella saxifraga* can develop. This community is transitional between the *Arrhenatheretum brizetosum* and the *Medicagini-Avenetum pubescentis*. Species occurring in 1994 which confirm a possible transition into that community are *Avenula pubescens*, *Bromus inermis*, *Cerastium arvense*, *Eryngium campestre*, *Leontodon hispidus*, *Leontodon saxatilis*, *Medicago falcata*, *Ononis repens ssp. spinosa* and *Plantago media*. According to Van der Zee (1992) this community is restricted to locations with clay percentage varying between 5-18%. This means that in the future on the experimental dike this community can only occur on locations with a clay percentage of <18%. On locations with a higher clay content the most obvious ultimate communities will be the *Arrhenatherum*, transition community of *Origanum vulgare* and *Euphorbia esula* [subass. group A / subass. group B] and the *Arrhenatheretum* subass. group A, variant with *Potentilla reptans* and *Galium mollugo*. Of course, these species-rich communities can only be reached under optimal management regimes. A relatively intensive grazing regime will ultimately probably lead to the *Lolio-Cynosuretum* subassociation *ononidetosum*. Seed sources and seed dispersal are crucial for these developments.

3.4.3 Flora before and after reconstruction

Almost all species found before the reconstruction were also recorded in the first four years after the reconstruction. The exceptions were *Knautia arvensis*, *Viola odorata* and *Ornithogalum umbellatum*. In 1991 a few flowering specimens of *Ornithogalum umbellatum* were found at two locations. This early-flowering species might have been overlooked previously. Before the reconstruction *Knautia arvensis* occurred in very small numbers at two locations on the experimental dike. The smaller the population of a species before the reconstruction, the lower the probability of re-occurrence after the reconstruction. The determination of *Viola odorata* might have been wrong. Four species survived in the spared zone only: *Calamagrostis epigejos*, *Peucedanum carvifolia*, *Rumex thyrsiflorus* and *Verbascum nigrum*. During the experiment the latter three dispersed to adjacent parts which consisted of replaced topsoil or imported clay.

These results support the conclusions of Ullmann and Heindl (1986) that although a species-rich vegetation may spontaneously develop, it is seldom a very rare community with a very high botanical value. This was confirmed by Zwaenepoel (1995) who found that the rarer and therefore often more appreciated species did not appear in newly sown verges, even though many other species successfully regenerated. The population size of many of the species that recovered after the reconstruction was much smaller than before the reconstruction. A relatively large number of species was recorded in the period 1987-1994 but not in 1978. Probably, some species were overlooked in the 1978 inventory. Additionally, the openness of the vegetation immediately after the reconstruction of the river dike probably offered many species a chance to germinate and (temporarily) establish in the vegetation. Seeds came from the seedbank and from dispersion from nearby by the wind, by the mowing machines or on the fleece of the sheep. There was a particularly striking increase in the *Leguminosae* (i.e. *Trifolium* sp., *Vicia* sp.) after the reconstruction. These species are able to store nitrogen from the air and use it to grow fast. In 1994, 50% of the 'new' species had already disappeared. Most of them were annuals. This decline in therophytes is probably due to their inability to compete with perennial grasses and herbs during later stages of succession (Down, 1973; in Kent & Coker, 1992). The species composition in the later stages and in the future will strongly depend on the management of the vegetation. Furthermore, the potential for the reintroduced species with small populations to spread will depend on their reaction to the management regime. The relation between vegetation, soil and management will be dealt with in the next chapter.

3.5 CONCLUSIONS

Between 1987-1994 after a large-scale reconstruction nine plant communities were distinguished on the experimental dike. In 1994, at the end of the experiment, only five more or less frequent communities remained, two communities had almost disappeared and two communities had already disappeared in 1990. In 1994, community I, the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus*, mainly occurring in the spared zone (see also Chapter 4), was still the best developed and most saturated *Arrhenatheretum elatioris* vegetation of all communities. Besides, this community had the largest proportion of rare to fairly common species (8.5%) and therefore the highest nature conservation interest. Only a very limited number of plots developed into this community. All of these were directly bordering the spared zone. This indicates the importance of the presence of a species-rich vegetation as a source of seeds. At the same time this indicates the slow dispersal rate of the species concerned.

Throughout the experiment the species diversity of community III, the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia*, was the highest of all communities distinguished. Furthermore, this second best developed community (after community I) increased from 39 species in 1987 to 46 in 1994. In 1994 the proportion of rare to fairly common species was already 3.2%.

On replaced sods, a negative change from a relatively species-rich vegetation to a species-poor vegetation, the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (community II) took place. Whereas in 1987 the species-rich, well-developed community III occurred in all plots on the replaced sods, in 1994 all plots except the plot with management hay-making twice a year were assigned to the community II. The species diversity of community II was low, mostly caused by a low number of herbs. Besides, community II contained a relatively large proportion of *Artemisietea* species. Generally, this community was found in permanent plots with bad management regimes (see also Chapter 4). This emphasizes the need of an optimal management after applying expensive methods of reconstruction like transplantation of complete sods.

The main succession stream started from a pioneer grassland, the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII), and from the community forming a transition between the *Arrhenatherion* and the *Eu-Polygono-Chenopodion* (comm. VIII) changing via the *Lolio-Cynosuretum* with *Crepis capillaris* en *Ranunculus repens* (VI) into the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). A switch from annual to perennial vegetation occurred within three years. The expansion of perennials at the expense of annuals is confirmed by the ordination diagrams in which the first axis is clearly related to a decrease of *Chenopodietea* and *Plantaginetea* species in combination with an increase of syntaxonomic elements of plant communities mainly consisting of perennials, in particular *Molinio-Arrhenatheretea*, *Artemisietea* and *Trifolion medii*. Additionally, the variation along the first axis of the ordination diagram was explained by the proportions of pasture species and hay meadow species and species of nitrogen-poor conditions. Community V, the *Arrhenatheretum* with dominance of *Alopecurus pratensis*, is a 'central' community from which the further development towards hay meadow communities or pasture communities can be expected, depending of the management regime applied. The species diversity of this community was relatively low, probably because of the dominance of the relatively tall grass species *Alopecurus pratensis*. Between 1990 and 1994 the diversity increased, which will consequently lead to a shift towards community III or community VI, which are respectively dependent on hay-making or grazing management (see also Chapter 4). Community VI, the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* was considered to be a transition between the *Arrhenatheretum* and the *Lolio-Cynosuretum*. In the future this community is likely to develop further under a grazing management regime to a well developed *Lolio-Cynosuretum*.

Seventeen stream valley species were found on the experimental dike. Only two of them, *Peucedanum carvifolia* and *Rumex thyrsiflorus*, were restricted to the spared zone immediately after the reconstruction. After 1987 they dispersed to bordering parts of the dike. The other species were also found in the replaced sods and on the replaced topsoil. This indicates the importance of the replaced sods and topsoil as a source of diaspores.

Changes in vegetation - caused by succession - mainly occur immediately after a reconstruction; after a few years the changes proceed much more slowly. Although a relatively high species diversity was reached in part of the experimental plots and a number of rare to fairly common species occurred between 1987 and 1994, the succession of the main part of the vegetation of the recently reconstructed river dikes to species-rich, well developed, relatively stable grasslands containing many rare species will probably take several more years.

Almost all the species found in 1978 were also recorded in the first four years after the reconstruction. Only two species, *Knautia arvensis* and *Viola odorata* had not reappeared by 1994. A relatively large number of species was recorded in the period 1987-1994 but not in 1978. Clearly, the openness of the vegetation immediately after the reconstruction of the river dike offered many species a chance to germinate and establish temporarily or permanently in the vegetation. The seed sources were the seedbank and dispersion from nearby, by wind, on the mowing machines and on the fleece of the sheep. The management of the vegetation will determine whether these new species will remain or will slowly dwindle and disappear when the vegetation closes. In 1994, 50% of the 'new' species had already disappeared. Most of them were annuals.

Appendix 1. Synoptic table of the communities distinguished. Percentage presence is given as well as mean cover (superscript). The percentage presence is expressed in six classes: + = 0-5%; I = 6-20%, II = 21-40%; III = 41-60%; IV = 61-80%; V = 81-100%. For calculation of mean cover the ordinal values are used. For explanation of the cluster numbers see the text.

Plant community	I	II	III	IV	V	VI	VII	VIII	IX
Number of relevés	66	61	89	23	226	203	117	18	5
Mean number of species	32	27	42	39	29	32	26	26	35
MOLINIO-ARRHENATHERETEA									
Cardamine pratensis	.	I^1	I^1	.	$+^1$	$+^1$	$+^1$	.	.
Centaurea jacea	IV^2	III^2	V^4	V^3	III^2	IV^2	II^1	I^1	I^1
Cerastium fontanum	I^1	.	II^1	II^1	I^1	I^1	II^1	II^1	.
Holcus lanatus	I^1	III^2	III^2	II^1	I^1	I^1	$+^1$	.	.
Plantago lanceolata	III^2	II^1	V^4	V^5	IV^3	V^4	V^3	III^2	V^4
Prunella vulgaris	.	.	I^1	II^1	$+^1$	I^1	$+^1$	.	.
Rumex acetosa	I^1	III^1	IV^3	II^1	III^1	II^1	I^1	I^1	II^1
Trifolium pratense	I^1	$+^1$	IV^3	V^4	III^2	V^3	IV^3	IV^2	.
Vicia cracca	IV^3	IV^3	V^4	V^3	IV^2	III^2	III^2	II^1	.
Constant companion species									
Festuca rubra	V^5	IV^3	V^6	V^5	V^5	V^5	IV^4	V^5	.
Poa pratensis	III^2	II^1	IV^3	III^2	IV^3	IV^3	II^1	.	.
Poa trivialis	IV^3	IV^3	IV^4	IV^3	IV^4	IV^3	III^2	IV^3	I^1
MOLINIETALIA									
Achillea ptarmica	.	.	.	.	$+^1$	$+^1$	.	I^1	.
Angelica sylvestris	.	$+^1$	I^1	I^1	$+^1$	$+^1$	.	.	.
Filipendula ulmaria	.	I^1	I^1	$+^1$	$+^1$	$+^1$	$+^1$	.	.
Lythrum salicaria	.	$+^1$	.	.	.	$+^1$	$+^1$	.	.
Phalaris arundinacea	$+^1$	III^2	II^1	II^2	I^1	$+^1$	$+^1$	.	.
Stachys palustris	.	.	I^1	$+^1$	.	$+^1$	.	.	.
Valeriana officinalis	.	III^2	III^1	I^1	$+^1$	$+^1$	$+^1$	.	.
ARRHENATHERION ELATIORIS									
Achillea millefolium	IV^3	II^1	V^3	IV^3	II^2	II^2	II^1	III^1	.
Alopecurus pratensis	IV^3	V^4	III^2	I^1	V^3	III^2	I^1	I^1	IV^2
Bellis perennis	.	.	III^2	II^1	$+^1$	II^1	I^1	.	.
Dactylis glomerata	V^4	V^5	V^5	V^5	V^5	V^5	IV^3	III^2	I^1
Festuca pratensis	I^1	I^1	II^1	II^1	I^1	I^1	I^1	I^1	I^1
Heracleum sphondylium	V^3	V^5	V^4	V^3	IV^3	III^1	II^1	II^1	.
Lathyrus pratensis	II^1	III^2	V^3	IV^3	II^1	I^1	I^1	II^1	I^1
Leucanthemum vulgare	.	$+^1$	IV^2	IV^3	I^1	II^1	I^1	.	.
Lotus corniculatus	.	I^1	II^1	II^1	I^1	II^1	I^1	I^1	.
Ranunculus acris	IV^2	III^2	V^4	V^4	IV^2	V^3	IV^2	III^1	III^1
Senecio jacobaea	I^1	$+^1$	III^2	II^1	II^1	III^2	I^1	I^1	I^1
Taraxacum officinale s.s.	II^1	I^1	III^2	IV^3	III^2	V^3	IV^2	IV^2	V^3
Trifolium dubium	I^1	.	II^1	II^1	II^1	II^1	II^1	.	.
Arrhenatheretum elatioris									
Arrhenatherum elatius	V^8	V^8	V^7	V^5	V^8	V^6	IV^3	II^1	II^1
Crepis biennis	I^1	I^1	III^2	IV^2	II^1	II^1	I^1	.	.
Daucus carota	II^1	$+^1$	II^1	II^1	II^1	III^2	II^1	II^1	.
Galium mollugo	V^4	V^3	IV^3	III^2	IV^2	III^2	II^1	.	I^1
Pastinaca sativa	I^1	.	$+^1$	.	I^1	$+^1$	$+^1$	II^1	.
Peucedanum carvifolia	III^2	$+^1$	.	.	$+^1$	$+^1$	$+^1$	.	.
Pimpinella major	.	.	.	.	.	$+^1$	.	.	.
Rumex thyrsiflorus	V^3	$+^1$	I^1	I^1	I^1	$+^1$	$+^1$	.	.
Tragopogon pratensis ssp. orient.	II^1	.	I^1	I^1	I^1	$+^1$	I^1	I^1	.
Trisetum flavescens	II^1	I^1	I^1	.	I^1	I^1	$+^1$	.	.
Differentiating species of Arrhenatheretum with respect to Lolio-Cynosuretum									
Anthriscus sylvestris	V^3	V^4	V^3	III^2	IV^3	III^1	III^2	V^2	I^1
Euphorbia esula	$+^1$	II^1	III^2	I^1	I^1	I^1	I^1	I^1	.
Heracleum sphondylium	V^3	V^5	V^4	V^3	IV^3	III^1	II^1	II^1	.
Symphytum officinale	IV^2	V^4	V^4	V^3	III^2	II^1	II^1	II^1	III^1

Arrhenatheretum elatioris subassociation group A (differentiating species)									
Alopecurus pratensis	IV^3	V^4	III^2	I^1	V^3	III^2	I^1	I^1	IV^2
Anthriscus sylvestris	V^3	V^4	V^3	III^2	IV^3	III^1	III^2	V^2	I^1
Glechoma hederacea	V^4	IV^3	V^4	III^2	IV^3	IV^3	II^1	II^1	I^1
Heracleum sphondylium	V^3	V^5	V^4	V^3	IV^3	III^1	II^1	II^1	.
Ranunculus repens	II^1	+^{1}	IV^2	V^3	III^2	V^3	V^3	V^4	IV^2
Arrhenatheretum elatioris alopecuretosum									
Cardamine pratensis	.	I^1	I^1	.	+^{1}	+^{1}	+^{1}	.	.
Lysimachia nummularia	.	I^1	IV^2	II^1	II^1	I^1	+^{1}	I^1	.
Ranunculus ficaria	.	+^{1}	.	.	.	.	.	.	.
Symphytum officinale	IV^2	V^4	V^4	V^3	III^2	II^1	II^1	II^1	III^1
Arrhenatheretum elatioris subassociation group B (differentiating species)									
Plantago media	.	.	I^1	+^{1}	.	+^{1}	.	.	.
Ranunculus bulbosus	.	.	I^1	+^{1}	I^1	II^1	I^1	.	.
Senecio erucifolius	.	II^1	II^1	III^2	+^{1}	+^{1}	.	.	.
Senecio jacobaea	I^1	+^{1}	III^2	II^1	II^1	III^2	I^1	I^1	I^1
Trisetum flavescens	II^1	I^1	I^1	.	I^1	I^1	+^{1}	.	.
Arrhenatheretum elatioris picridetosum									
Agrimonia eupatoria	+^{1}	.	+^{1}	.	+^{1}	+^{1}	.	.	.
Carduus crispus	III^2	II^1	II^1	I^1	I^1	I^1	II^1	I^1	III^1
Cichorium intybus	I^1	.	I^1	I^1	I^1	II^1	I^1	I^1	II^1
Pastinaca sativa	I^1	.	+^{1}	.	I^1	+^{1}	+^{1}	II^1	.
Peucedanum carvifolia	III^2	+^{1}	.	.	+^{1}	+^{1}	+^{1}	.	.
Tragopogon pratensis ssp. orient.	II^1	.	I^1	I^1	I^1	+^{1}	I^1	I^1	.
Arrhenatheretum elatioris brizetosum									
Agrostis capillaris	.	.	+^{1}	.	.	+^{1}	.	.	.
Anthoxanthum odoratum	I^1	+^{1}	I^1	+^{1}	I^1	I^1	+^{1}	.	.
Bromus hordeaceus	+^{1}	.	I^1	.	I^1	I^1	I^1	II^1	.
Crepis capillaris	+^{1}	.	I^1	I^1	I^1	III^2	I^1	.	.
Hypochaeris radicata	.	.	+^{1}	.	.	+^{1}	+^{1}	.	.
Lolio Cynosuretum									
Phleum pratense	III^2	I^1	III^2	V^4	III^2	IV^3	V^5	V^6	IV^3
Lolio-Cynosuretum (characteristic combination)									
Bellis perennis	.	.	III^2	II^1	+^{1}	II^1	I^1	.	.
Crepis capillaris	+^{1}	.	I^1	I^1	I^1	III^2	I^1	.	.
Geranium molle	+^{1}	+^{1}	+^{1}	I^1	+^{1}	+^{1}	I^1	I^1	I^1
Juncus articulatus	.	.	.	.	.	+^{1}	+^{1}	.	.
Leontodon autumnalis	.	.	+^{1}	.	+^{1}	+^{1}	.	.	I^1
Leontodon saxatilis	.	.	+^{1}	.	.	.	.	.	.
Lolium perenne	III^3	I^1	IV^4	V^7	IV^3	V^6	V^8	V^9	II^3
Phleum pratense	III^2	I^1	III^2	V^4	III^2	IV^3	V^5	V^6	IV^3
Trifolium repens	I^1	.	IV^2	V^4	II^1	V^4	V^4	V^6	IV^2
Lolio-Cynosuretum subassociation group A (diff. taxa)									
Agrostis capillaris	.	.	+^{1}	.	.	+^{1}	.	.	.
Anthoxanthum odoratum	I^1	+^{1}	I^1	+^{1}	I^1	I^1	+^{1}	.	.
Festuca rubra	V^5	IV^3	V^6	V^5	V^5	V^5	IV^4	V^5	.
Holcus lanatus	I^1	III^2	III^2	II^1	I^1	I^1	+^{1}	.	.
Lolio-Cynosuretum luzuletosum campestris									
Festuca rubra	V^5	IV^3	V^6	V^5	V^5	V^5	IV^4	V^5	.
Hypochaeris radicata	.	.	+^{1}	.	.	+^{1}	+^{1}	.	.
Lotus corniculatus	.	I^1	II^1	II^1	I^1	II^1	I^1	I^1	.
Trifolium dubium	I^1	.	II^1	II^1	II^1	II^2	II^1	.	.
Lolio-Cynosuretum subassociation group B (diff. taxa)									
Agrostis stolonifera	I^1	II^1	III^2	V^4	II^2	IV^3	II^1	I^1	.
Carex spicata	.	.	.	.	+^{1}	+^{1}	.	.	.
Cirsium arvense	IV^2	V^5	V^3	V^3	V^3	V^3	III^2	V^2	IV^1
Dactylis glomerata	V^4	V^5	V^5	V^5	V^5	V^5	IV^3	III^2	I^1
Potentilla reptans	V^3	III^2	V^3	V^3	IV^3	IV^3	III^2	I^1	II^2
Trisetum flavescens	II^1	I^1	I^1	.	I^1	I^1	+^{1}	.	.

Lolio-Cynosuretum plantaginetosum mediae									
Cirsium vulgare	I^{1}	+^{1}	II^{1}	IV^{2}	II^{1}	III^{1}	II^{1}	.	.
Medicago lupulina	I^{1}	.	III^{2}	V^{3}	II^{1}	IV^{3}	IV^{2}	IV^{2}	I^{1}
Plantago media	.	.	I^{1}	+^{1}	.	+^{1}	.	.	.
Ranunculus bulbosus	.	.	I^{1}	+^{1}	I^{1}	II^{1}	I^{1}	.	.
Lolio-Cynosuretum ononidetosum									
Carduus nutans	.	.	+^{1}	I^{1}	.	+^{1}	+^{1}	.	.
Cichorium intybus	I^{1}	.	I^{1}	I^{1}	I^{1}	II^{1}	I^{1}	I^{1}	II^{1}
Cirsium vulgare	I^{1}	+^{1}	II^{1}	IV^{2}	II^{1}	III^{1}	II^{1}	.	.
Convolvulus arvensis	IV^{3}	+^{1}	+^{1}	.	II^{1}	II^{1}	I^{1}	.	.
Eryngium campestre	.	.	I^{1}	I^{1}	.	+^{1}	.	.	.
Medicago lupulina	I^{1}	.	III^{2}	V^{3}	II^{1}	IV^{3}	IV^{2}	IV^{2}	I^{1}
Plantago media	.	.	I^{1}	+^{1}	.	+^{1}	.	.	.
Ranunculus bulbosus	.	.	I^{1}	+^{1}	I^{1}	II^{1}	I^{1}	.	.
Verbena officinalis	.	.	.	.	+^{1}	I^{1}	.	.	.
KOELERIO-CORYNEPHORETEA & FESTUCO-BROMETEA (diff. taxa)									
Allium oleraceum	+^{1}	.	.	.	.	.	.	.	.
Avenula pubescens	III^{2}	I^{1}	II^{1}	.	+^{1}	+^{1}	+^{1}	.	.
Cerastium arvense	I^{1}	.	.	.	+^{1}	.	+^{1}	.	.
Ranunculus bulbosus	.	.	I^{1}	+^{1}	I^{1}	II^{1}	I^{1}	.	.
KOELERIO-CORYNEPHORETEA									
Campanula rotundifolia	.	.	+^{1}	.	+^{1}	+^{1}	.	.	.
Hypericum perforatum	+^{1}	+^{1}	+^{1}	+^{1}	.	+^{1}	.	.	.
Veronica arvensis	.	.	.	.	.	.	.	.	II^{1}
FESTUCO-BROMETEA									
Eryngium campestre	.	.	I^{1}	I^{1}	.	+^{1}	.	.	.
Leontodon hispidus	.	.	.	.	+^{1}	I^{1}	+^{1}	I^{1}	.
Plantago media	.	.	I^{1}	+^{1}	.	+^{1}	.	.	.
Medicagini-Avenetum pubescentis									
Bromus inermis	+^{1}	+^{1}	+^{1}	+^{1}	+^{1}	+^{1}	.	.	.
Calamagrostis epigejos	I^{1}	+^{1}	.	.	.	.	.	.	.
Eryngium campestre	.	.	I^{1}	I^{1}	.	+^{1}	.	.	.
Medicago falcata	I^{1}	.	+^{1}	.	+^{1}	+^{1}	+^{1}	.	.
TRIFOLIO-GERANIETEA SANGUINEA alliance **TRIFOLION MEDII**									
Agrimonia eupatoria	+^{1}	.	+^{1}	.	+^{1}	+^{1}	.	.	.
Dactylis glomerata	V^{4}	V^{5}	V^{5}	V^{5}	V^{5}	V^{5}	IV^{3}	III^{2}	I^{1}
Glechoma hederacea	V^{4}	IV^{3}	V^{4}	III^{2}	IV^{3}	IV^{3}	II^{1}	II^{1}	I^{1}
Hypericum perforatum	+^{1}	+^{1}	+^{1}	+^{1}	.	+^{1}	.	.	.
Lathyrus pratensis	II^{1}	III^{2}	V^{3}	IV^{3}	II^{1}	I^{1}	I^{1}	II^{1}	I^{1}
Lathyrus tuberosus	.	.	.	.	.	+^{1}	.	.	.
Senecio erucifolius	.	II^{1}	II^{1}	III^{2}	+^{1}	+^{1}	.	.	.
Senecio jacobaea	I^{1}	+^{1}	III^{2}	II^{1}	II^{1}	III^{2}	I^{1}	I^{1}	I^{1}
Verbascum nigrum	III^{2}	+^{1}	.	.	+^{1}	.	+^{1}	.	.
Veronica chamaedrys	II^{1}	I^{1}	III^{2}	+^{1}	II^{1}	I^{1}	I^{1}	.	.
Vicia sepium	III^{2}	IV^{3}	V^{4}	IV^{3}	II^{1}	I^{1}	II^{1}	I^{1}	.
PLANTAGINETEA MAJORIS association **Lolio-Plantaginetum** (characteristic combination)									
Capsella bursa-pastoris	I^{1}	.	+^{1}	+^{1}	+^{1}	+^{1}	II^{1}	III^{2}	V^{5}
Lolium perenne	III^{3}	I^{1}	IV^{4}	V^{7}	IV^{3}	V^{6}	V^{8}	V^{9}	II^{3}
Plantago major	+^{1}	.	I^{1}	II^{1}	+^{1}	II^{1}	III^{2}	V^{3}	.
Poa annua	.	.	.	.	+^{1}	I^{1}	I^{1}	I^{1}	V^{8}
Polygonum aviculare	+^{1}	.	.	.	+^{1}	I^{1}	II^{1}	V^{4}	V^{3}
Taraxacum officinale s.s.	II^{1}	I^{1}	III^{2}	IV^{3}	III^{2}	V^{3}	IV^{2}	IV^{2}	V^{3}
PLANTAGINETEA MAJORIS association **Poo-Lolietum** (characteristic combination)									
Carex hirta	II^{1}	I^{1}	I^{1}	I^{1}	I^{1}	I^{1}	I^{1}	.	.
Elymus repens	V^{6}	V^{6}	V^{5}	V^{5}	V^{6}	V^{5}	IV^{3}	II^{2}	V^{3}
Leontodon autumnalis	.	.	+^{1}	.	+^{1}	+^{1}	.	.	I^{1}
Lolium perenne	III^{3}	I^{1}	IV^{4}	V^{7}	IV^{3}	V^{6}	V^{8}	V^{9}	II^{3}
Plantago major	+^{1}	.	I^{1}	II^{1}	+^{1}	II^{1}	III^{2}	V^{3}	.
Poa pratensis	III^{2}	II^{1}	IV^{3}	III^{2}	IV^{3}	IV^{3}	II^{1}	.	.
Poa trivialis	IV^{3}	IV^{3}	IV^{4}	IV^{3}	IV^{4}	IV^{3}	III^{2}	IV^{3}	I^{1}
Potentilla anserina	.	I^{1}	I^{1}	I^{1}	I^{1}	+^{1}	I^{1}	II^{1}	.
Pulicaria dysenterica	.	I^{1}	II^{1}	III^{3}	+^{1}	+^{1}	+^{1}	.	.

Ranunculus repens	II^1	$+^1$	IV^2	V^3	III^2	V^3	V^3	V^4	IV^2
Rorippa sylvestris	.	.	.	I^1	$+^1$	$+^1$	I^1	II^2	V^4
Rumex crispus	II^1	III^2	III^1	IV^2	III^1	II^1	III^1	IV^2	V^2
Taraxacum officinale s.s.	II^1	I^1	III^2	IV^3	III^2	V^3	IV^2	IV^2	V^3
Trifolium hybridum	$+^1$	.	II^1	III^2	I^1	III^2	III^2	.	.
Trifolium repens	I^1	.	IV^2	V^4	II^1	V^4	V^4	V^6	IV^2
Tussilago farfara	.	.	$+^1$	I^1	$+^1$	$+^1$	$+^1$	.	.
ARTEMISIETEA VULGARIS									
Carduus crispus	III^2	II^1	II^1	I^1	I^1	I^1	II^1	I^1	III^1
Galium aparine	.	II^1	$+^1$	.	I^1	$+^1$	$+^1$	.	.
Rumex obtusifolius	II^1	II^1	IV^2	IV^2	III^2	III^1	III^2	II^1	V^2
Urtica dioica	III^2	V^4	II^1	.	II^1	I^1	I^1	.	.
ARTEMISIETALIA VULGARIS									
Arctium pubens	$+^1$	.	.	.	$+^1$	$+^1$	I^1	I^1	.
Artemisia vulgaris	I^1	I^1	$+^1$	.	$+^1$	I^1	I^1	I^1	.
Brassica nigra	.	$+^1$	$+^1$	.	$+^1$	.	.	.	II^1
Bromus sterilis	$+^1$	$+^1$	.	.	I^1	$+^1$	.	.	.
Calystegia sepium	I^1	II^1	II^1	I^1	II^1	II^1	II^1	.	II^1
Carduus crispus	III^2	II^1	II^1	I^1	I^1	I^1	II^1	I^1	III^1
Carex spicata	.	.	.	.	$+^1$	$+^1$	.	.	.
Cirsium arvense	IV^2	V^3	V^3	V^3	V^3	V^3	III^2	V^2	IV^1
Cirsium vulgare	I^1	$+^1$	II^1	IV^2	II^1	III^1	II^1	.	.
Cruciata laevipes	.	$+^1$	$+^1$	.	.	.	.	.	.
Glechoma hederacea	V^4	IV^3	V^4	III^2	IV^3	IV^3	II^1	II^1	I^1
Lamium album	V^3	III^2	$+^1$	.	I^1	I^1	I^1	I^1	.
Lapsana communis	$+^1$	.	.	.	.	.	$+^1$	.	.
Lathyrus tuberosus	.	.	.	.	.	$+^1$	.	.	.
Linaria vulgaris	$+^1$	I^1	I^1	I^1	$+^1$	I^1	$+^1$	I^1	.
Melilotus altissima	.	$+^1$	I^1	II^1	$+^1$	.	I^1	I^1	.
Rubus caesius	IV^3	IV^3	IV^2	III^1	II^1	II^1	II^1	.	III^1
Silene dioica	.	.	.	.	.	$+^1$	.	.	.
Silene latifolia ssp. alba	.	$+^1$	.	.	$+^1$	$+^1$	.	.	.
Tanacetum vulgare	IV^3	II^1	I^1	I^1	I^1	I^1	I^1	I^1	.
Urtica dioica	III^2	V^4	II^1	.	II^1	I^1	I^1	.	.
Verbena officinalis	.	.	.	.	$+^1$	I^1	.	.	.
Vicia sepium	III^2	IV^3	V^4	IV^3	II^1	I^1	II^1	I^1	.
CHENOPODIETEA									
Capsella bursa-pastoris	I^1	.	$+^1$	$+^1$	$+^1$	$+^1$	II^1	III^2	V^5
Chenopodium album	$+^1$	.	$+^1$	$+^1$	$+^1$	$+^1$	I^1	IV^2	V^5
Senecio vulgaris	$+^1$	.	$+^1$	$+^1$	$+^1$	$+^1$	I^1	I^1	III^2
Solanum nigrum	.	.	.	.	.	.	$+^1$	.	II^1
Sonchus asper	$+^1$	$+^1$	I^1	II^1	$+^1$	I^1	II^1	III^2	IV^4
Sonchus oleraceus	$+^1$	.	$+^1$	$+^1$	$+^1$	I^1	I^1	I^1	II^1
Stellaria media	II^1	I^1	I^1	$+^1$	I^1	I^1	II^1	III^2	V^4
CHENOPODIETEA alliance **POLYGONO-CHENOPODION**									
Anagallis arvensis ssp. arvensis	.	.	.	.	.	$+^1$	$+^1$	I^1	I^1
Bidens tripartita	$+^1$	.	.	.	.	.	.	.	.
Chenopodium rubrum	.	.	.	.	.	.	.	.	I^1
Equisetum arvense	II^1	I^1	III^2	IV^2	I^1	I^1	I^1	I^1	.
Erodium cicutarium	.	.	.	.	.	.	.	.	I^1
Fumaria officinalis	.	.	.	.	.	.	.	.	I^1
Juncus bufonius	.	.	.	.	.	$+^1$	.	.	.
Matricaria maritima	I^1	$+^1$	I^1	II^1	$+^1$	I^1	III^2	V^5	III^2
Polygonum amphibium	II^1	IV^2	IV^2	V^3	III^1	II^1	III^2	III^1	IV^2
Sonchus arvensis var. arvensis	.	.	$+^1$	$+^1$	$+^1$	$+^1$	.	.	.
Thlaspi arvense	.	$+^1$	.	.	.	.	$+^1$	.	I^1
CHENOPODIETEA suballiance **EU-POLYGONO-CHENOPODION**									
Euphorbia helioscopia	.	.	.	.	$+^1$	$+^1$	$+^1$	.	V^3
Geranium dissectum	I^1	I^1	II^1	II^1	II^2	II^2	II^1	I^1	III^2
Lamium purpureum	.	.	.	.	$+^1$	$+^1$	.	.	V^3
Polygonum persicaria	$+^1$	.	$+^1$	$+^1$	.	$+^1$	I^1	II^1	IV^2
Sonchus asper	$+^1$	$+^1$	I^1	II^1	$+^1$	I^1	II^1	III^2	IV^4
Veronica agrestis	.	.	.	.	$+^1$	.	.	.	.
Veronica persica	.	.	.	.	$+^1$	$+^1$	.	.	.

CHENOPODIETEA alliance SISYMBRION									
Bromus sterilis	$+^{1}$	$+^{1}$	.	.	I^{1}	$+^{1}$	.	.	.
Erigeron canadensis	.	.	$+^{1}$	$+^{1}$	$+^{1}$	.	I^{1}	.	.
Lactuca serriola	$+^{1}$	$+^{1}$	$+^{1}$	$+^{1}$	$+^{1}$	$+^{1}$	$+^{1}$	.	.
Linaria vulgaris	$+^{1}$	I^{1}	I^{1}	I^{1}	$+^{1}$	I^{1}	$+^{1}$	I^{1}	.
Sisymbrium officinale	.	.	.	.	.	.	$+^{1}$	I^{1}	.
CHENOPODIETEA alliance POLYGONO–CORONOPION									
Capsella bursa-pastoris	I^{1}	.	$+^{1}$	$+^{1}$	$+^{1}$	$+^{1}$	II^{1}	III^{2}	V^{5}
Matricaria discoidea	.	.	.	.	.	.	.	II^{1}	III^{1}
Polygonum aviculare	$+^{1}$	.	.	.	$+^{1}$	I^{1}	II^{1}	V^{4}	V^{3}
CHENOPODIETEA alliance ONOPORDION ACANTHII									
Carduus nutans	.	.	$+^{1}$	I^{1}	.	$+^{1}$	$+^{1}$	.	.
Reseda lutea	.	$+^{1}$	$+^{1}$	.	.	$+^{1}$	.	I^{1}	.
Verbascum nigrum	III^{2}	$+^{1}$	.	.	$+^{1}$	.	$+^{1}$	.	.
SECALIETEA									
Matricaria recutita	.	.	.	.	$+^{1}$	$+^{1}$	$+^{1}$	II^{1}	II^{1}
Myosotis arvensis	$+^{1}$	$+^{1}$	I^{1}	.	$+^{1}$	.	.	.	.
Papaver dubium	.	.	.	.	.	$+^{1}$	$+^{1}$	.	.
Papaver rhoeas	.	.	.	$+^{1}$	.	.	.	.	I^{1}
Polygonum convolvulus	.	.	.	.	$+^{1}$	.	$+^{1}$	.	I^{1}
Sinapis arvensis	.	I^{1}	I^{1}	I^{1}	I^{1}	$+^{1}$	I^{1}	II^{1}	V^{4}
Viola arvensis	.	.	.	.	.	$+^{1}$	.	.	.
Remaining Species									
Aegopodium podagraria	.	$+^{1}$	I^{1}	.	.	.	.	.	.
Allium vineale	II^{1}	II^{1}	II^{1}	$+^{1}$	II^{1}	I^{1}	I^{1}	.	II^{1}
Alopecurus geniculatus	.	.	.	.	.	$+^{1}$	.	.	.
Cardamine hirsuta	.	.	.	.	$+^{1}$	.	.	.	.
Carex acuta	.	.	.	.	$+^{1}$	$+^{1}$	.	.	.
Crataegus monogyna	.	.	$+^{1}$	.	$+^{1}$	.	.	.	.
Festuca arundinacea	II^{1}	IV^{3}	IV^{4}	III^{2}	II^{1}	II^{1}	I^{1}	.	.
Festuca ovina	.	.	.	.	.	$+^{1}$	.	.	.
Galeopsis tetrahit	.	$+^{1}$	.	$+^{1}$	$+^{1}$	.	$+^{1}$	.	.
Hordeum secalinum	.	.	.	.	$+^{1}$	.	.	.	.
Hypericum dubium	.	.	$+^{1}$	.	.	.	.	.	.
Juncus effusus	.	.	.	.	.	$+^{1}$	.	.	.
Lathyrus species	.	.	.	.	.	$+^{1}$	.	.	.
Lolium multiflorum	.	.	.	.	I^{1}	II^{2}	$+^{1}$	.	.
Lycopus europaeus	.	.	.	.	$+^{1}$	.	$+^{1}$	.	.
Mentha aquatica	.	.	.	.	.	$+^{1}$	.	.	.
Mentha arvensis	.	.	.	.	$+^{1}$	.	.	.	.
Ornithogalum umbellatum	.	.	$+^{1}$	.	.	.	.	.	.
Phragmites australis	.	I^{1}	I^{1}	I^{1}	I^{1}	$+^{1}$	$+^{1}$	.	I^{1}
Poa angustifolia	$+^{1}$	$+^{1}$	.	.	.	.	.	.	.
Potentilla norvegica	.	.	.	.	$+^{1}$	$+^{1}$	.	.	.
Rorippa palustris	.	.	.	.	.	$+^{1}$	.	.	.
Rosa canina	I^{1}	.	.	.	.	.	.	.	.
Rumex x pratensis	I^{1}	I^{1}	I^{1}	$+^{1}$	I^{1}	$+^{1}$	.	.	.
Salix aurita	.	.	.	.	.	$+^{1}$	.	.	.
Salix cinerea	.	.	.	.	.	.	$+^{1}$	.	.
Salix viminalis	.	.	.	.	.	$+^{1}$	.	.	.
Scrophularia nodosa	$+^{1}$	.	.	.	$+^{1}$	$+^{1}$	$+^{1}$	.	.
Stellaria aquatica	.	.	.	.	$+^{1}$	$+^{1}$	$+^{1}$	.	I^{1}
Tragopogon pratensis ssp. prat.	$+^{1}$	.	.	.	.	.	.	.	.
Triticum aestivum	$+^{1}$	.	.	.	.	.	I^{1}	I^{1}	.
Valerianella locusta	$+^{1}$	$+^{1}$	.	.	.	.	.	.	.
Veronica hederifolia	.	.	.	.	$+^{1}$	.	.	.	.
Vicia hirsuta	.	.	.	.	$+^{1}$	.	.	.	.
Vicia sativa ssp. *nigra*	III^{2}	II^{1}	III^{2}	I^{1}	IV^{2}	III^{2}	II^{2}	II^{1}	II^{1}

CHAPTER 4

VEGETATION DEVELOPMENT BETWEEN 1987 AND 1994 UNDER DIFFERENT RECONSTRUCTION AND MANAGEMENT PRACTICES

With K.V. Sýkora

4.1 INTRODUCTION

Reconstruction

The qualitative and quantitative deterioration of the low-productive, species rich grasslands in the Netherlands has emphasized the need to restore these ecosystems. This problem also occurs in other countries and the European Community is now stimulating both the restoration and management of these grasslands (Jordan III *et al.*, 1987). A great deal is already known about the functioning and management of low-productive, species-rich grasslands (Duffey *et al.*, 1974; Rorison & Hunt, 1980; Bakker, 1989). However, less is known about how to restore these communities, i.e. how to develop them for example after the reconstruction of Dutch river dikes.

The immigration of plant species by seed dispersal (Verkaar *et al.*, 1983b; Marshall, 1988) and germination and seedling establishment (Grubb, 1977; Bakker *et al.*, 1980; Silvertown, 1981; Verkaar *et al.*, 1983a) are important regeneration characteristics. River dikes lose their seedbank during reconstruction, so species have to immigrate from the surroundings. However, because species-rich river dike vegetation is very scarce nowadays, it takes a long time for species to colonize the reconstructed dikes and consequently for the vegetation to develop. Sparing a part of the vegetation can provide a source from which species can disperse to the reconstructed parts of the dike. The vegetation development can be accelerated by replacing the former top layer, which contains propagules of the former vegetation. This can be done by replacing complete sods manually or by replacing the topsoil by machine.

The species-rich grasslands typical of river dikes require special soil conditions (Yodzis, 1978; Sýkora & Liebrand, 1987, 1988; Van der Zee, 1992). These conditions can be approximated during dike reconstructions by replacing the original topsoil (Sýkora & Liebrand, 1992). Additionally, because there are propagules in the topsoil, the replacement of the topsoil allows the re-appearance and accelerated redevelopment of species-rich grasslands. It were these propagules that enabled almost all the pre-reconstruction species to recolonize the experimental river dike after reconstruction (Liebrand, 1993). Imported clay may have different soil characteristics which may lead to differences in the species composition of the future vegetation. Furthermore, the vegetation development on this clay will be considerably retarded because of the lack of propagules.

It is not only the material the dike is built from that is altered during the reconstruction, but also the slope and its aspect. Both are important for the redevelopment of the vegetation (Grime & Lloyd, 1973; Van Heerden, 1979; Smith, 1980; Sýkora & Liebrand, 1988).

Sowing

A dense vegetation hampers germination and establishment (Grime, 1973, 1979; Grime *et al.*, 1981). Therefore, the sowing density after a reconstruction is important for the subsequent development of the vegetation, especially if persistent grass species are sown. A dense pure stand of *Lolium perenne* restricts the germination and establishment of indigenous species. Applying seed mixtures containing seeds of the former vegetation can accelerate the vegetation development. These seeds have to be collected just before the reconstruction. The sowing strategy on the reconstructed dike can also be considered to be part of the reconstruction. In spite of this, in this research the sowing was examined separately.

Management

In Europe authentic natural grassland has for long been restricted to sites unsuitable for woodland: in the mountains above the tree line, peat moors, natural moors, areas along rivers and natural pastures grazed by wild animals. Only after the introduction of livestock farming in Europe 7,000-10,000 years ago did semi-natural grasslands start to occur over larger areas. Obviously, hayfields cut twice or more yearly are no older than 1000 years (Ellenberg, 1978). In the Netherlands about 60% of the total flora is nowadays restricted to semi-natural plant communities (Van der Maarel, 1975). Like all semi-natural landscape elements, river dike grasslands developed under the influence of mankind (Knapp, 1979). Mowing and grazing the dike slopes discourages shrubs and trees. The removal of the mowings and the leaching of the soil removed nutrients from the ecosytem and in the absence of fertilization, the soil became impoverished. This enabled the development of very species-rich grasslands containing many rare species (Green, 1983).

4.2 METHODS

In order to restore former species-rich plant communities on an experimental river dike several methods of reconstruction, sowing mixtures and management practices were applied (see Chapter 2 for a description). The impact of the methods of reconstruction was investigated by describing the succession. Several species attributes and community characteristics can be used to explain successional sequences such as life-forms, rarity, species richness and phytosociological composition (see Chapter 3).

On one hand the impact of method of reconstruction, sowing and management on the change in the vegetation between 1987 and 1994 was studied (chapter 4) and on the other hand the relation between the species composition as present in 1994 and these factors was analysed (chapter 5).

4.2.1 Ascertaining the vegetation development between 1987 and 1994

The development between 1987 and 1994 was ascertained by comparing data on 209 permanent plots in 1987, 1990, 1992 and 1994. In 1987, one year after the reconstruction, the vegetation composition of all methods of reconstruction differed, whereas within a method of reconstruction the vegetation was approximately homogeneous. Directly after the reconstruction the composition of the vegetation mainly depends on the method of reconstruction applied and the sowing rate and composition of the seed mixtures applied. The soil within a method of reconstruction was regarded as homogeneous in 1987 and the vegetation as not yet influenced by management. The different management practices were applied from 1987, and therefore in 1987 the vegetation of each method of reconstruction in 1987 could be described by representative relevés. The 82 relevés examined in 1987 represented the starting situations of 172 permanent plots which were analysed in 1990, 1992 and 1994. Sections A and B were reconstructed in 1987, a year later than the other sections, and therefore the vegetation in 37 permanent quadrats in these sections was first analysed in 1988. Thus in 1994 the vegetation development in these sections had lasted only 7 years, compared with 8 years in the other sections. This should be borne in mind when considering the vegetation development.

In all 209 permanent plots the following factors were analysed in 1987, 1990, 1992 and 1994: species richness, proportions (%) of the phytosociological syntaxa (weighted by cover abundances of the species), proportions (%) (weighted) of the main phytosociological groups and proportions (%) of the 9 plant communities (see Chapter 3).

Effect of method of reconstruction

In order to study the effect of the reconstruction on the vegetation composition, the percentage distribution of permanent plots among the nine plant communities in the separate reconstruction methods in 1987, 1990, 1992 and 1994 was analysed. Subsequently the shifts in plant communities of the permanent quadrats between 1987 and 1994 were analysed in relation to the five reconstruction methods. Sections G2, G2' and E2 were also examined separately, to determine the impact of the spared zone and the replaced sods.

Effect of sowing
Within each of the reconstruction methods all sowings were analysed separately. Per sowing the proportions in terms of percentage of the plant communities were recorded in 1987, 1990, 1992 and 1994. Subsequently the shifts in plant communities of the permanent quadrats between 1987 and 1994 were analysed in relation to the separate sowings.

Effect of management
The management practices were divided into four main categories; mowing, grazing, burning and no management. The impact of the management on the vegetation composition in 1987, 1990, 1992 and 1994 was examined by determining the proportions of the plant communities in the four main management categories in the separate years. These calculations were also done within each method of reconstruction and also with each management practice, within each method of reconstruction and also ignoring the method of reconstruction.

Dividing the proportions of the plant communities in 1994 by the proportions in 1987 supplies a measure of the decrease or increase in the number of relevés within the plant communities. A value higher than 1.00 indicates an increase in 1994 compared with 1987, a value lower than 1.00 indicates a decrease. As the main change in the vegetation between 1987 and 1994 was the shifting of relevés from the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V), only the quotients of these plant communities were used. The larger the increase in community V and the larger the decrease in community VII, the faster the development from community VII to community V. The quotients which indicated increase in community V and decrease in community VII were used to rank the management practices by speed of development.

4.2.2 Above-ground biomass and annual crop production

At 93 locations (92 on the experimental dike and 1 in a dry floodplain grassland vegetation) the above-ground biomass of the vegetation (kg dry matter ha^{-1}) was measured one or more times a year in 1988, 1989, 1990, 1992 and 1994, just before mowing or grazing. The biomass in unmown plots was determined at the same time, to allow a comparison. Exclusion cages were used for measuring the biomass production in the meadows. These cages were moved each year. The biomass in spring (i.e. peak standing crop) at all locations could be compared. Additionally, the total production per year of locations managed twice a year was obtained by totalling both measured values.

The above-ground biomass was measured by clipping the vegetation just above the ground surface in 4 randomly chosen sub-plots of (25 x 25) cm^2 in each of the permanent quadrats, including standing dead material, and excluding litter and bryophytes. Dry weights were measured after drying at 70°C for 48 h.

In many studies, biomass is defined as 'peak standing crop' (maximum above-ground biomass) in July. In the present study the biomass was measured in June and September, so the peak standing crop was not measured. According to Oomes (1992) the peak standing crop is 62% (± 5%) of the year production. In this research the year production was determined at 137 locations (40 in 1988, 46 in 1989 and 51 in 1990). When calculating the proportion of the spring production in the annual production, the spring production measured was compared with the peak standing crop. To trace if there was any change in this percentage (spring production/year production * 100%) between 1988 and 1990, this percentage was determined in 37 locations managed twice yearly in 1988, 1989 and 1990. Of these locations, 29 were mown twice a year and 8 were grazed twice a year or mown and grazed once a year.

The mean biomass in June (i.e. peak standing crop) and the annual biomass production were calculated per plant community, per method of reconstruction, per seed mixture applied and per management practice.

4.2.3 Statistics

ANOVA was used to explore separately the relationship between the dependent variables considered in this chapter and the independent variables plant community, method of reconstruction, sowing and management (see also § 2.4). All data sets appeared to be normally distributed. Differences are tested with a oneway ANOVA followed by a Least Significance Difference (LSD) test. Treatments which are significally different are assigned to different homogeneous groups. Homogeneous groups with one or more characters in common are not significantly different.

4.3 RESULTS

4.3.1 Impact of method of reconstruction, sowing and management on plant communities between 1987 and 1994

Relation between methods of reconstruction and plant communities
Throughout the monitoring period (1987-1994) all permanent plots on the spared zone belonged to the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) (see table 28).

Table 28. Percentage distribution of the relevés among the plant communities in the methods of reconstruction in 1987, 1990, 1992 and 1994.

Method of reconstr.	Year	N	Plant community I	II	III	IV	V	VI	VII	VIII	IX
Spared zone	1987	8	100	.	.	.	.	.	.	.	.
	1990	8	100	.	.	.	.	.	.	.	.
	1992	8	100	.	.	.	.	.	.	.	.
	1994	8	100	.	.	.	.	.	.	.	.
Replaced sods	1987	4	.	.	100	.	.	.	.	.	.
	1990	4	.	50	50	.	.	.	.	.	.
	1992	4	.	50	25	.	25	.	.	.	.
	1994	4	.	75	25	.	.	.	.	.	.
Replaced topsoil	1987	96	2	.	7	9	10	24	44	1	2
	1990	96	3	10	26	9	22	24	5	.	.
	1992	96	4	19	25	2	29	17	4	.	.
	1994	96	5	22	24	1	34	14	.	.	.
Replaced subsoil	1987	33	.	.	.	.	.	55	39	.	6
	1990	33	.	.	.	.	9	67	24	.	.
	1992	33	.	.	.	.	42	52	6	.	.
	1994	33	.	.	.	.	61	39	.	.	.
Imported clay	1987	65	2	.	.	.	.	2	43	52	2
	1990	65	8	.	.	5	28	43	17	.	.
	1992	65	6	2	.	6	51	29	6	.	.
	1994	65	8	3	5	2	54	25	5	.	.

The vegetation in the four permanent plots where complete sods were replaced by hand belonged to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) in 1987. In 1994 three of the four permanent plots belonged to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II), whereas one permanent plot still belonged to vegetation type III.

In 1987 most of the permanent plots on replaced topsoil belonged to the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) (44%) and the *Arrhenatheretum* with *Crepis capillaris* and *Ranunculus repens* (VI) (24%). In 1990 most permanent plots belonged to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (26%), the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) (24%) and the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) (22%). The proportion of the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) had decreased (5%). In 1990 the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) appeared on the replaced topsoil. In 1994 the majority of the 96 permanent plots on topsoil belonged to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) (34%), the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) (24%) and the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) (22%). In 1994 the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) disappeared. Throughout the monitoring period a small number of permanent plots on topsoil belonged to the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I). These plots were always on replaced topsoil in the section with the spared zone. This suggests that species dispersed from the spared zone to the replaced topsoil.

The vegetation development on subsoil that had been replaced as a new top layer was very slow. In 1994 most of the permanent plots on subsoil (61%) belonged to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) and 39% to the *Arrhenatheretum* with *Crepis capillaris* and *Ranunculus repens* (VI).

In 1987 most of the permanent plots on imported clay belonged to the association fragment community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) and the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) (52% and 43% respectively). In 1990 most of the plots (43%) belonged to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI). Whereas the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) was not even present in 1987, in 1992 most of the permanent plots on imported clay belonged to this plant community (51%). From the beginning of the experiment a small number of permanent plots belonged to the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I). These plots were all situated in the section with the spared zone. This implies that species dispersed from the spared zone to the imported clay. Clearly the chemical and physical composition of both the replaced topsoil and the imported clay is suitable for the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I).

In 1994 three permanent plots on imported clay developed to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). These plots were all situated in the section where complete sods were replaced. They were all located directly below the sods replaced manually. Except from the section with the spared zone, in no other permanent plot on imported clay was the development so advanced in 1994 as it was directly below the sods replaced manually.

Relation between sowing and plant communities

The spared zone and the replaced complete sods were not seeded at all. For this reason the permanent plots in these parts are not considered in this chapter. Table 29 shows that only on replaced topsoil the permanent plots sown with D1+LGM developed to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) in 1994. In all other permanent plots the development did not go further than the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). By 1994, all permanent plots on replaced topsoil sown with only LGM (i.e. locally gathered mixture) had developed to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). By then, three of the seven permanent plots sown with LGM in combination with *Lolium multiflorum* (LGM+Lm) still belonged to the *Arrhenatheretum* with *Crepis capillaris* and *Ranunculus repens* (VI). In 1994 one of the ten permanent plots that had not been sown was assigned to the *Arrhenatheretum* with *Crepis capillaris* and *Ranunculus repens* (VI) compared with five of the ten permanent plots sown with BG5. On replaced topsoil, sowing with LGM led to the fastest development, followed by no sowing. Sowing with *Lolium multiflorum* and with BG5 retarded the development.

Table 29. Percentage distribution of the relevés among the plant communities in the combinations of method of reconstruction and sowing in 1987, 1990, 1992 and 1994.

Method of recon.	Sowing	Year	N	Plant community I	II	III	IV	V	VI	VII	VIII	IX
Replaced topsoil	None	1987	10	.	.	.	.	.	80	.	.	20
		1990	10	.	.	.	.	10	90	.	.	.
		1992	10	.	.	.	.	70	30	.	.	.
		1994	10	.	.	.	.	90	10	.	.	.
	LGM	1987	4	.	.	.	.	50	50	.	.	.
		1990	4	.	.	.	.	50	25	25	.	.
		1992	4	.	.	.	.	50	50	.	.	.
		1994	4	.	.	.	.	100	.	.	.	.
	D1+LGM	1987	56	.	.	13	16	13	13	46	.	.
		1990	56	.	13	45	16	23	4	.	.	.
		1992	56	.	27	43	4	25	2	.	.	.
		1994	56	.	30	41	2	21	6	.	.	.
	BG5	1987	8	.	.	.	.	.	.	100	.	.
		1990	8	.	.	.	.	.	50	50	.	.
		1992	8	.	.	.	.	.	50	50	.	.
		1994	8	.	.	.	.	50	50	.	.	.
	Lm+LGM	1987	7	.	.	.	.	14	86	.	.	.
		1990	7	.	.	.	.	29	71	.	.	.
		1992	7	.	.	.	.	43	57	.	.	.
		1994	7	.	.	.	.	57	43	.	.	.
Replaced subsoil	None	1987	10	.	.	.	.	.	80	.	.	20
		1990	10	.	.	.	.	20	80	.	.	.
		1992	10	.	.	.	.	80	20	.	.	.
		1994	10	.	.	.	.	90	10	.	.	.
	LGM	1987	4	.	.	.	.	.	75	25	.	.
		1990	4	.	.	.	.	25	75	.	.	.
		1992	4	.	.	.	.	50	50	.	.	.
		1994	4	.	.	.	.	75	25	.	.	.
	BG5+LGM	1987	7	.	.	.	.	.	.	100	.	.
		1990	7	.	.	.	.	.	43	57	.	.
		1992	7	.	.	.	.	29	71	.	.	.
		1994	7	.	.	.	.	57	43	.	.	.
	BG5	1987	5	.	.	.	.	.	.	100	.	.
		1990	5	.	.	.	.	.	20	80	.	.
		1992	5	.	.	.	.	.	60	40	.	.
		1994	5	.	.	.	.	40	60	.	.	.
	Lm+LGM	1987	7	.	.	.	.	.	100	.	.	.
		1990	7	.	.	.	.	.	100	.	.	.
		1992	7	.	.	.	.	29	71	.	.	.
		1994	7	.	.	.	.	29	71	.	.	.
Imported clay	D1+LGM	1987	28	.	.	.	.	.	.	4	96	.
		1990	28	.	.	.	.	36	50	14	.	.
		1992	28	.	.	.	.	64	36	.	.	.
		1994	28	.	.	.	.	79	21	.	.	.
	D1	1987	9	.	.	.	.	.	11	89	.	.
		1990	9	.	.	.	.	.	89	11	.	.
		1992	9	.	.	.	.	22	67	11	.	.
		1994	9	.	.	.	.	22	67	11	.	.
	BG5	1987	3	.	.	.	.	.	.	100	.	.
		1990	3	.	.	.	.	.	.	100	.	.
		1992	3	.	.	.	.	.	.	100	.	.
		1994	3	.	.	.	.	.	33	67	.	.

In 1994 most of the permanent plots on replaced subsoil that were unsown or had been sown with LGM or BG5+LGM belonged to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V).

Most permanent plots sown with BG5 and Lm+LGM belonged to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI). In 1994 nine of the ten permanent plots on replaced subsoil that were not sown belonged to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) and one to the *Arrhenatheretum* with *Crepis capillaris* and *Ranunculus repens* (VI). This proportion was 3:1 for the plots sown with LGM and 2:5 for the plots sown with LGM in combination with *Lolium multiflorum*. For the sowing with BG5 in combinatie with LGM this proportion was 4:3 and for sowing with only BG5 it was 2:3. On subsoil, no sowing led to the fastest development, followed by sowing with a locally gathered mixture. Sowing with *Lolium multiflorum* and with BG5 retarded the development.

In 1994 most of the permanent plots on imported clay sown with D1+LGM belonged to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V), whereas most permanent plots sown solely with D1 belonged to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI). The development of permanent plots sown with BG5 was retarded. Two of the three plots still belonged to the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII).

Relation between management and plant communities

From 1987 to 1994 all permanent plots in the spared zone belonged to the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) irrespective of the management applied (see appendix 1 on page 107). Only mowing management practices were applied on the spared zone.

In 1987 all the permanent plots on the replaced complete sods belonged to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). In 1994 three of the four plots belonged to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) (see appendix 1). The management of these plots was mulching twice a year, hay-making in September and hay-making once every two years. In 1994 only the plot mown twice a year with removal of the mowings still belonged to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). There were no grazed plots on the replaced sods. All permanent plots on replaced topsoil and imported clay belonging to the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) were located in the section with the spared zone. All permanent plots on imported clay belonging to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) were located in the section with the replaced complete sods. It is reasonable to assume that the effect of the dispersal of the species from the spared zone and the replaced sods to the neighbouring parts of the improved dike exceeds the effect of management in these sections. For this reason the permanent plots in these sections are not considered in the remainder of this chapter. Table 30 and appendix 1 show the proportions (as percentages) of the vegetation types over the main management practices per method of reconstruction. The vegetation development on replaced subsoil and on imported clay did not go further than the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). In contrast to this, in 1987 the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) and the *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV) were already occurring on replaced topsoil. After 1987 the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) also occurred on replaced topsoil.

In 1987 most of the permanent plots on replaced topsoil belonged to the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) (see table 30). Hay-making twice a year and hay-making in June in combination with mulching in September encouraged a development to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) (47% and 67% repectively) (see appendix 1). None of the plots with those management practices developed to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II). Plots mulched twice a year also developed to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) (33%) but also to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) (25%). Hay-making once a year gave nearly similar results regardless of whether it was performed in June or in September, except for one plot mown in June that still belonged to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) in 1994. Most of the plots with hay-making once in two years developed to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) (55%). In 1994 many plots that had only been grazed developed from the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) (Gseas: 40%, 2xG: 50%). Only a few grazed plots developed to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). None of the grazed plots developed to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II). In 1994 the burned plots and the plots without management all developed to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II).

Table 30. Distribution (%) of the relevés among the plant communities in the combinations of method of reconstruction and the main management practices in 1987 to 1994. The sections with the spared zone and the replaced sods are not included.

Method of recon.	Manage- ment	Year	N	Plant community I	II	III	IV	V	VI	VII	VIII	IX
Replaced topsoil	Mowing	1987	59	.	.	10	10	12	29	36	.	3
		1990	59	.	9	34	10	17	22	9	.	.
		1992	59	.	19	31	2	29	14	7	.	.
		1994	59	.	22	32	.	42	3	.	.	.
	Grazing	1987	22	.	.	.	9	14	23	55	.	.
		1990	22	.	.	18	14	32	36	.	.	.
		1992	22	.	.	27	5	41	27	.	.	.
		1994	22	.	.	18	5	36	41	.	.	.
	Burning	1987	2	.	.	50	50	.	.	.	.	.
		1990	2	.	50	50	.	.	.	.	.	.
		1992	2	.	100	.	.	.	.	.	.	.
		1994	2	.	100	.	.	.	.	.	.	.
	No manag.	1987	2	.	.	.	.	.	50	50	.	.
		1990	2	.	50	.	.	50	.	.	.	.
		1992	2	.	100	.	.	.	.	.	.	.
		1994	2	.	100	.	.	.	.	.	.	.
Replaced subsoil	Mowing	1987	27	.	.	.	.	.	56	37	7	.
		1990	27	.	.	.	.	11	59	30	.	.
		1992	27	.	.	.	.	48	44	7	.	.
		1994	27	.	.	.	.	74	26	.	.	.
	Grazing	1987	6	.	.	.	.	.	50	50	.	.
		1990	6	.	.	.	.	.	100	.	.	.
		1992	6	.	.	.	.	17	83	.	.	.
		1994	6	.	.	.	.	.	100	.	.	.
Imported Clay	Mowing	1987	22	.	.	.	.	.	.	23	77	.
		1990	22	.	.	.	.	45	55	.	.	.
		1992	22	.	.	.	.	82	18	.	.	.
		1994	22	.	.	.	.	86	14	.	.	.
	Grazing	1987	17	.	.	.	.	.	6	35	59	.
		1990	17	.	.	.	.	.	53	47	.	.
		1992	17	.	.	.	.	6	71	23	.	.
		1994	17	.	.	.	.	23	59	18	.	.
	No manag	1987	1	.	.	.	.	.	.	100	.	.
		1990	1	.	.	.	.	.	100	.	.	.
		1992	1	.	.	.	.	100	.	.	.	.
		1994	1	.	.	.	.	100	.	.	.	.

In 1987 nearly all permanent plots on former subsoil belonged to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) and the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII). In 1994 they all belonged to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) and the *Lolio-Cynosuretum* with *Crepis capillaris* and

Ranunculus repens (VI). Only the mown plots developed to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). All grazed plots belonged to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI).

Table 31. Percentage distribution of the relevés among the plant communities in the different management practices in 1987, 1990, 1992 and 1994.

Management	N	Year	Plant communities I	II	III	IV	V	VI	VII	VIII	IX
2xM+r	38	1987	8	.	5	3	8	18	40	8	11
		1990	16	.	13	11	11	37	13	.	.
		1992	13	.	18	5	40	18	5	.	.
		1994	11	.	24	.	58	8	.	.	.
2xM-r	28	1987	7	.	7	4	7	21	39	14	.
		1990	7	4	21	7	21	29	11	.	.
		1992	7	7	14	4	36	29	4	.	.
		1994	7	21	18	.	39	14	.	.	.
2xM+-r	10	1987	10	.	10	10	.	20	20	30	.
		1990	10	.	20	.	40	30	.	.	.
		1992	10	10	20	.	60	.	.	.	.
		1994	20	10	20	.	50	.	.	.	.
1xM+r-el	14	1987	7	.	7	7	7	29	36	7	.
		1990	14	7	21	7	7	44	.	.	.
		1992	14	14	21	.	21	30	.	.	.
		1994	14	22	14	.	36	14	.	.	.
1xM+r-lt	34	1987	9	.	6	3	3	27	38	15	.
		1990	9	9	12	6	29	27	9	.	.
		1992	12	9	9	3	56	6	6	.	.
		1994	18	12	9	3	53	6	.	.	.
1xM+r/2y	24	1987	4	.	8	4	.	17	46	17	4
		1990	4	21	8	.	33	17	17	.	.
		1992	4	38	.	4	38	13	4	.	.
		1994	4	33	8	.	50	4	.	.	.
Gseas	14	1987	.	.	.	.	7	7	57	29	.
		1990	.	.	7	.	14	50	29	.	.
		1992	.	.	7	.	14	71	7	.	.
		1994	.	.	7	.	14	71	7	.	.
2xG	14	1987	.	.	.	7	.	14	50	29	.
		1990	.	.	14	7	7	58	14	.	.
		1992	.	.	7	7	36	43	7	.	.
		1994	.	.	7	7	29	50	7	.	.
G+M	12	1987	.	.	.	.	9	25	33	33	.
		1990	.	.	.	8	25	42	25	.	.
		1992	.	.	17	.	25	50	8	.	.
		1994	.	.	.	.	25	67	8	.	.
M+G	15	1987	.	.	.	7	7	20	46	20	.
		1990	.	.	7	7	20	59	7	.	.
		1992	.	.	13	.	27	53	7	.	.
		1994	.	.	13	.	47	40	.	.	.
Burning	2	1987	.	.	50	50	.	.	.	.	.
		1990	.	50	50	.	.	.	.	.	.
		1992	.	100	.	.	.	.	.	.	.
		1994	.	100	.	.	.	.	.	.	.
No manag.	3	1987	.	.	.	.	.	33	67	.	.
		1990	.	33	.	.	33	33	.	.	.
		1992	.	67	.	.	33	.	.	.	.
		1994	.	67	.	.	33	.	.	.	.

In 1987 all permanent plots on imported clay, except one, belonged to the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) and the fragment community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII). In 1994 the mown plots had developed mainly to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) whereas the grazed plots developed mainly to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI). The unmanaged plot developed from the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V).

In 1987 most of the permanent plots belonged to the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII), in spite of the management (see table 31). In 1994 most mown plots belonged to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V), whereas most of the grazed plots belonged to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI), except for those mown in June and grazed in September. All the plots that still belonged to the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) in 1994 were grazed. The burned plots and 2 of the 3 unmanaged permanent plots had developed to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) in 1994. The proportion of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) was relatively high in the hay-making twice a year treatment (24%) and in the hay-making in June in combination with mulching in September treatment (20%). The proportion of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) was relatively high in the hay-making once every two years in September treatment (33%) but also in the treatments of mulching twice a year (21%) and of hay-making once a year in June (22%). The proportion of the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) was relatively high in the hay-making once a year in September treatment (18%) and in the hay-making in June in combination with mulching in September treatment (20%). Whereas the proportional amount of the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) increased at hay-making in June in combination with mulching in September and at hay-making once a year in September, it decreased slightly in the hay-making twice a year treatment.

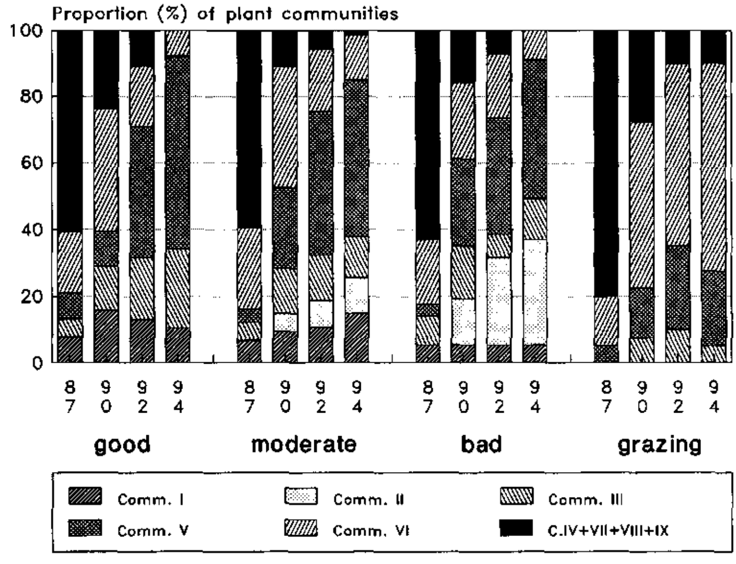


Figure 13. Proportion of the plant communities in the management qualification groups in 1987, 1990, 1992 and 1994.

The most important (i.e. most frequent) change in the vegetation between 1987 and 1994 was the shift from the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). The vegetation in grazed permanent plots shifted from community VII to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI).

In figure 13 the proportions of the plant communities in the management qualification groups in the different years are shown (see also § 4.4.4, page 90). Under good management (hay-making twice a year) the proportion of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) increased from 5% in 1987 to 24% in 1994. Under bad management (mulching twice a year, hay-making once every two years, burning, no management) the proportion of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) increased from 0% in 1987 to 32% in 1994. Under moderate management (hay-making in June with mulching in September, hay-making in June, hay-making in September, hay-making in June with grazing in September) the proportion of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) increased from 0% in 1987 to 11% in 1994. On the grazed permanent plots (grazing throughout the summer, grazing twice a year, grazing in June with hay-making in September) the proportion of the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) increased sharply from 15% in 1987 to 63% in 1994.

4.3.2 Above-ground biomass and annual crop production

Biomass of the plant communities

Table 32 shows the peak standing crop (PSC) of the plant communities in 1988, 1990, 1992 and 1994. After 1990 plant communities VIII and IX were absent (see Chapter 3). Plant communities IV and VII had also practically disappeared in 1994; in that year community IV was represented by only 2 permanent plots, community VII by only 3 permanent plots. Community II first appeared in 1990.

Table 32. Mean peak standing crop per plant community in 1987, 1990, 1992 and 1994. LSD-test: homogeneous groups at $p<0.05$ level.

1988 Plant comm.	Peak standing crop (ton ha^{-1})	Homogeneous groups	1990 Plant comm.	Peak standing crop (ton ha^{-1})	Homogeneous groups
VIII	2.990	a .	IV	2.785	a . . .
VII	3.367	a .	VII	2.952	a b . .
V	3.555	a .	III	5.406	. b c .
VI	4.461	a .	VI	5.755	. . c .
IV	4.926	a b	I	6.841	. . c d
III	6.757	. b	V	7.450	. . . d
I	6.929	. b	II	7.953	. . . d

1992 Plant comm.	Peak standing crop (ton ha^{-1})	Homogeneous groups	1994 Plant comm.	Peak standing crop (ton ha^{-1})	Homogeneous groups
IV	3.228	a . . .	IV	4.196	a . .
VI	6.051	a b . .	III	5.874	a . .
III	6.228	a b . .	VI	6.210	a b .
VII	6.353	a b c .	VII	7.061	a b c
V	7.241	. b c .	I	7.348	. b c
II	8.180	. . c d	V	7.526	. . c
I	9.379	. . . d	II	8.316	. . c

In 1988 the peak standing crop (PSC) of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) and the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex* *thyrsiflorus* (I) was significantly ($p<0.05$) larger than of communities V to VIII. In 1990 the PSC of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) and the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) was significantly larger compared with community III, the *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV), the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) and the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII). In 1992 the PSC of communities I and II was significantly larger compared with communities III, IV and VI. In 1994 the PSC of communities III, IV and VI were significantly smaller compared with communities II and V. In that year the biomass of community I was significantly larger compared with communities III and IV.

Effect of method of reconstruction

Only permanent plots with the management treatment hay-making twice a year were considered here. In general, the mean peak standing crop under this management increased between 1988 and 1994 (see figure 14). Although the peak standing crop in the spared zone fluctuated between 1988 and 1994, in 1994 it was almost equal to the value measured in 1988. On replaced topsoil the maximum peak standing crop occurred as early as 1989 whereas on complete sods, on replaced subsoil and on imported clay it was still increasing in 1994.

In 1994 the largest biomass in June was measured on the replaced complete sods and the smallest biomass on the replaced topsoil (table 33). The differences between the methods of reconstruction were not significant ($p<0.05$), due to the small number of observations.

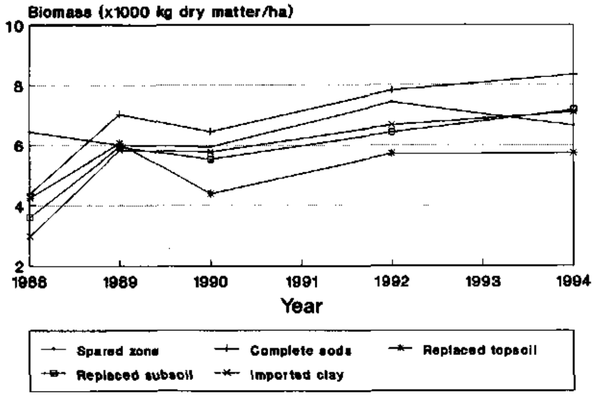


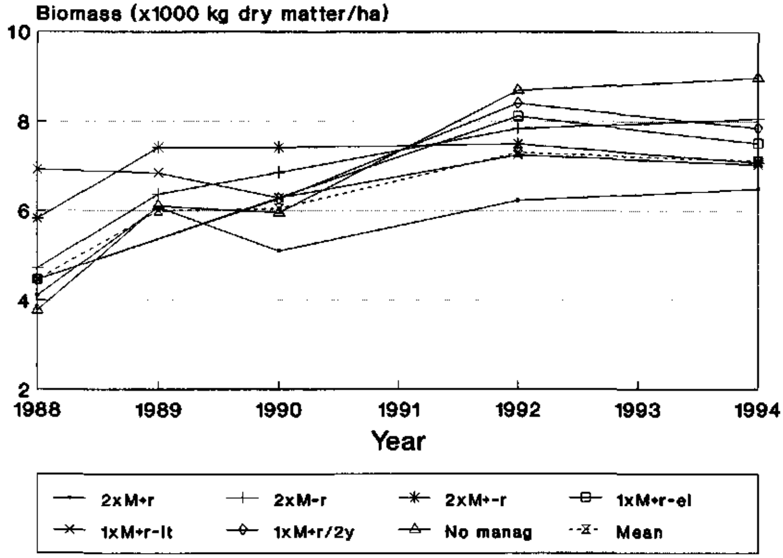
Figure 14. Mean peak standing crop (biomass in June) per method of reconstruction between 1988 and 1994.

Table 33. Mean peak standing crop per method of reconstruction at management 2xM+r in 1994.

Method of reconstr.	Biomass ton/ha
Spared zone	6.648
Sods	8.352
Topsoil	5.741
Subsoil	7.168
Imp. clay	7.101

Effect of management

In general, between 1988 and 1992 the peak standing crop (PSC) on the experimental dike increased (see figure 15). Between 1992 and 1994 it stabilized or slightly decreased in the mowing treatments. Under grazing twice a year, burning and 'no management' the PSC increased and under both combinations of mowing and grazing the PSC decreased between 1992 and 1994. In 1988 and 1989 differences in peak standing crop were not yet significant. In 1990 burning led to a significantly ($p<0.05$) larger PSC than grazing twice a year and mowing twice a year with removal of the hay. Mowing once every 2 years and 'no management' led in 1992 to a significant larger PSC than mowing twice a year with removal of the hay and grazing twice a year.



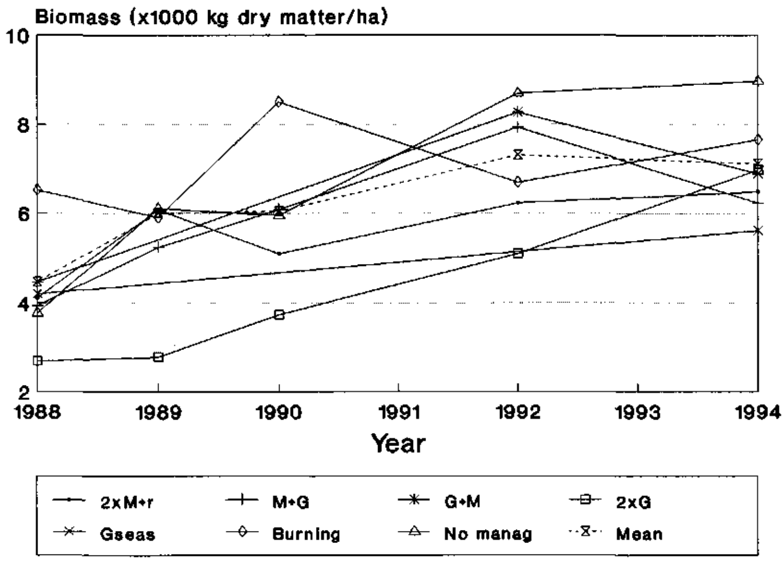


Figure 15. Peak standing crop (biomass in June) per management strategy between 1988 and 1994. For the sake of clearness the results are represented in two figures. The management hay-making twice a year (2xM+r) is included in both figures.

4.3.3 Impact of method of reconstruction, sowing and management on species richness between 1987 and 1994

Relation between method of reconstruction and species richness

All methods of reconstruction contained one or more permanent plots under the management strategies hay-making twice a year (2xM+r), mulching twice a year (2xM-r), hay-making once a year in September (1xM+r-lt) and hay-making once every two years in September (1xM+r/2y). In the spared zone and on the complete sods only one quartet of those management practices was implemented whereas on the other methods of reconstruction 4 to 10 quartets were implemented. Each quartet consisted of 4 permanent plots. Species richness data on these four management practices were used to compare the species richness of the different methods of reconstruction. Table 34 shows the mean numbers of species in 1987 to 1994 in the different methods of reconstruction. In general, the mean species richness decreased between 1987 and 1990 and increased between 1990 and 1994. In 1987 species richness on imported clay was significantly lower than in all other methods of reconstruction. In 1990 the species richness on imported clay was only significantly lower than on complete sods and topsoil and in 1992 it was significantly lower than on subsoil, in the spared zone and on topsoil. In 1994 the species richness on imported clay and complete sods was significantly lower than in the spared zone and on the subsoil. Although the complete sods had the greatest species richness in 1987, by 1994 they had the least species richness.

Table 34. Mean number of species per method of reconstruction in 1987, 1990, 1992 and 1994. Only management treatments 2xM+r, 2xM-r, 1xM+r-lt and 1xM+r/2y are involved. LSD-test: homogeneous groups at p<0.05 level.

Year	Method of reconstr.	Species N	Homogeneous groups
1987	Sods	36.8	a .
	Sp. zone	34.0	a .
	Topsoil	33.5	a .
	Subsoil	33.3	a .
	Imp. clay	25.4	. b
	mean	*30.4*	
1990	Sods	34.5	a .
	Topsoil	30.4	a .
	Subsoil	28.0	a b
	Sp. zone	26.5	a b
	Imp. clay	25.1	. b
	mean	*28.2*	
1992	Subsoil	34.3	a .
	Sp. zone	33.0	a .
	Topsoil	30.9	a .
	Sods	29.3	a b
	Imp. clay	27.1	. b
	mean	*30.2*	
1994	Sp. zone	38.5	a .
	Subsoil	37.8	a .
	Topsoil	34.5	a b
	Imp. clay	32.6	. b
	Sods	32.0	. b
	mean	*34.5*	

Relation between sowing and species richness

Data of species richness of the four most frequent mowing practices (2xM+r, 2xM-r, 1xM+r-lt, 1xM+r/2y) were used to compare the species richness of the different sowings. Table 35 shows the mean numbers of species in 1987 to 1994 of the different sowings. In general, the mean species richness decreased between 1987 and 1990, except from sowing with D1, and increased between 1990 and 1994. Sowing with BG5 showed an especially sharp decrease between 1987 and 1990. In 1987 species richness in sowing D1 was significantly lower (LSD-test: p<0.05)

Table 35. Mean number of species per sowing. Only the four most frequent mowing practices are considered.

Sowing	n	Mean number of species 1987	1990	1992	1994
No sowing	8	35.4	30.5	31.1	35.3
LGM	8	32.5	27.8	35.3	38.0
D1	4	18.5	29.5	31.5	35.0
D1+LGM	56	30.2	28.7	28.6	33.4
BG5	8	31.5	22.9	28.9	35.3
BG5+LGM	4	31.2	26.0	34.0	38.5
Lm+LGM	8	32.8	28.9	34.5	35.1
Total	96	30.4	28.2	30.2	34.5

than in sowings with D1+LGM, LGM, Lm+LGM, BG5 and 'no sowing'. Additionally, no sowing led to significantly more species than D1+LGM and BG5+LGM. In 1990, 1992 and 1994 the differences in species richness between the sowings were no longer significant.

To exclude the effect of the method of reconstruction, in table 36 topsoil, subsoil and imported clay are shown separately. In 1987 species richness was by far the lowest in sowing D1 on imported clay. Adding LGM to D1 led to a significant (LSD-test: $p<0.05$) increase of 8 species in 1987. In the other years the differences were no longer significant. The negative effect of sowing with BG5 was only visible between 1987 and 1990, especially on replaced topsoil. In 1990, species richness in sowing with BG5 was significantly ($p<0.05$) lower than in sowing with D1+LGM. Thereafter, the species richness increased as it did in all other sowings. In 1994 there were no longer any significant differences in species richness.

Table 36. Mean number of species on replaced topsoil and subsoil and imported clay. Only the four most frequent mowing practices are considered.

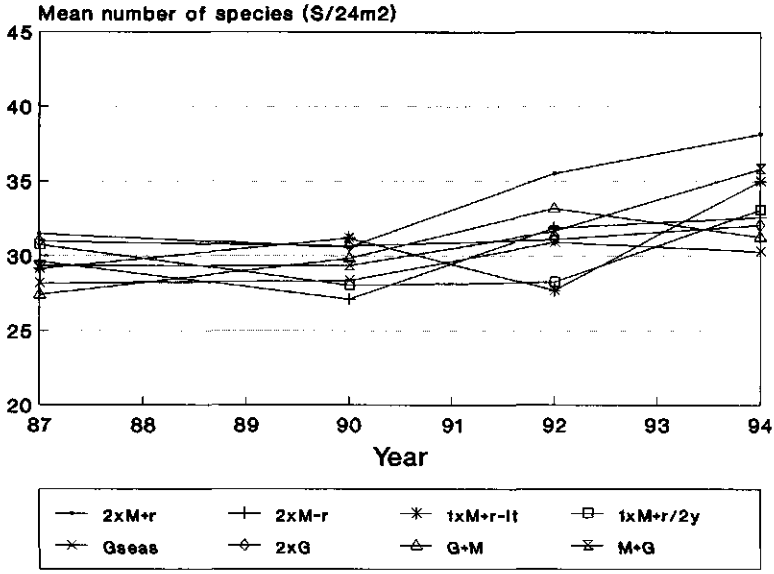
Method of reconstr.	Sowing	n	Mean number of species			
			1987	1990	1992	1994
Topsoil	LGM	4	26.7	26.5	35.3	37.0
	D1+LGM	28	34.5	32.9	30.7	34.5
	BG5	4	32.0	19.8	25.0	32.3
	Lm+LGM	4	32.0	26.8	33.8	34.8
Subsoil	LGM	4	38.3	29.0	35.3	39.0
	BG5	4	31.0	26.0	32.8	38.3
	BG5+LGM	4	31.2	26.0	34.0	38.5
	Lm+LGM	4	33.7	31.0	35.3	35.5
Imported clay	D1	4	18.5	29.5	31.5	35.0
	D1+LGM	28	26.4	24.4	26.5	32.3

Management

Table 37 shows the mean numbers of species of all management practices applied in 1987 to 1994. The relatively high numbers of species in plots with management burning and no management in 1987 are attributable to the small numbers of permanent plots under these management strategies and the high degree of disturbance in these plots. Figure 16 shows the relation between the management and the species richness between 1987 and 1994.

Table 37. Mean number of species in the various management practices in 1987, 1990, 1992 and 1994.

Management	n	Mean number of species			
		1987	1990	1992	1994
2xM+r	38	31.5	30.6	35.5	38.2
2xM-r	28	29.6	27.1	31.9	32.6
2xM+-r	10	27.5	23.5	33.2	34.7
1xM+r-el	14	30.5	29.1	32.1	34.6
1xM+r-lt	34	29.1	31.2	27.7	35.0
1xM/2y+r	24	30.8	28.0	28.3	33.0
Gseas	14	28.2	28.4	30.9	30.3
2xG	14	31.0	30.7	31.1	32.1
G+M	12	27.4	29.8	33.2	31.3
M+G	16	29.4	29.4	31.6	35.8
burning	2	40.5	35.0	24.0	26.5
no manag.	3	37.0	36.0	28.3	31.7
Total	209	30.5	29.5	31.3	34.1



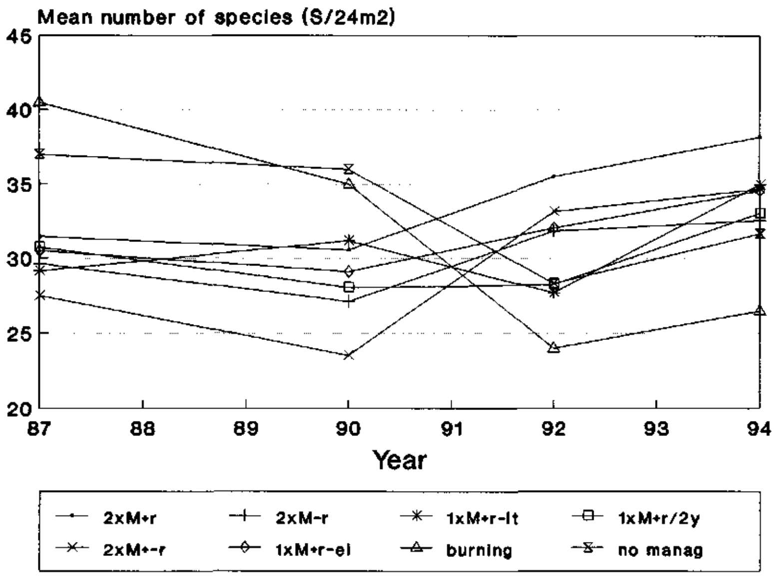


Figure 16. Relation between mean number of species and management in 1987, 1990, 1992 and 1994. For the sake of clearness the results are represented in two figures. The management treatments hay-making twice a year, mulching twice a year, hay-making in September and hay-making once every two years are included in both figures.

With the exception of the management practices burning and 'no management', the species richness of the management strategies did not differ very much in 1987. Differences only appeared after 1990. In 1992 species richness under hay-making twice a year was significantly (LSD-test: $p<0.05$) higher than in most other management practices (see table 38). In 1994 species richness under hay-making twice a year was significantly higher than under hay-making once every two years, mulching twice a year, grazing twice a year, grazing in spring in combination with hay-making in September, grazing throughout the summer, burning and no management.

Table 38. Mean number of species per management strategy in 1992 and 1994. LSD-test: homogeneous groups at p<0.05 level.

1992 Management	Mean species number	Homogeneous groups	1994 Management	Mean species number	Homogeneous groups
2xM+r	35.5	a . .	2xM+r	38.2	a .
G+M	33.2	a b .	M+G	35.8	a b
2xM+-r	33.2	a b .	1xM+r-1t	35.0	a b
1xM+r-el	32.1	a b .	2xM+-r	34.7	a b
2xM-r	31.9	. b .	1xM+r-el	34.6	a b
M+G	31.6	. b c	1xM+r/2y	33.0	. b
2xG	31.1	. b c	2xM-r	32.6	. b
Gseas	30.9	. b c	2xG	32.1	. b
No manag	28.3	. b c	No manag	31.7	. b
1xM+r/2y	28.3	. b c	G+M	31.3	. b
1xM+r-1t	27.7	. . c	Gseas	30.3	. b
Burning	24.0	. . c	Burning	26.5	. b

In table 39 the same numbers of permanent plots were used to compare the most frequent mowing practices. Whereas in 1987 and 1990 the mean numbers of species under these four management practices were almost equal, in 1992 and 1994 the number of species under hay-making twice a year was significantly higher (LSD-test: $p<0.05$) than under the other management strategies.

Table 39. Mean number of species of the four most frequent mowing practices in 1987, 1990, 1992 and 1994.

Management	n	mean number of species 1987	1990	1992	1994
2xM+r	24	30.5	29.0	35.5	39.6
2xM-r	24	29.6	26.1	30.3	31.1
1xM+r-1t	24	30.4	29.7	26.8	34.2
1xM+r/2y	24	30.8	28.0	28.3	33.0
Total	96	30.4	28.2	30.2	34.5

4.3.4 Effect of the management on the level of species

The effect of the management between 1987 and 1994 was determined for all species. Figures 17 to 23 show the abundance of *Arrhenatherum elatius*, *Lolium perenne*, *Cirsium arvense*, *Cirsium vulgare*, *Crepis biennis*, *Crepis capillaris* and *Centaurea jacea* per management strategy in 1987, 1990, 1992 and 1994. For the sake of clearness the results of each species are represented in two figures. The first figure contains the mowing treatments, burning and no management, the second figure contains two hay-making treatments, two grazing treatments and two combinations of grazing and hay-making. Hay-making twice a year and hay-making in September are included in both figures.

Arrhenatherum elatius was favoured by mowing practices (see figure 17), whereas *Lolium perenne* was favoured by grazing (see figure 18). Grazing throughout the summer led to the lowest abundance of *Arrhenatherum elatius* but to the highest abundance of *Lolium perenne*.

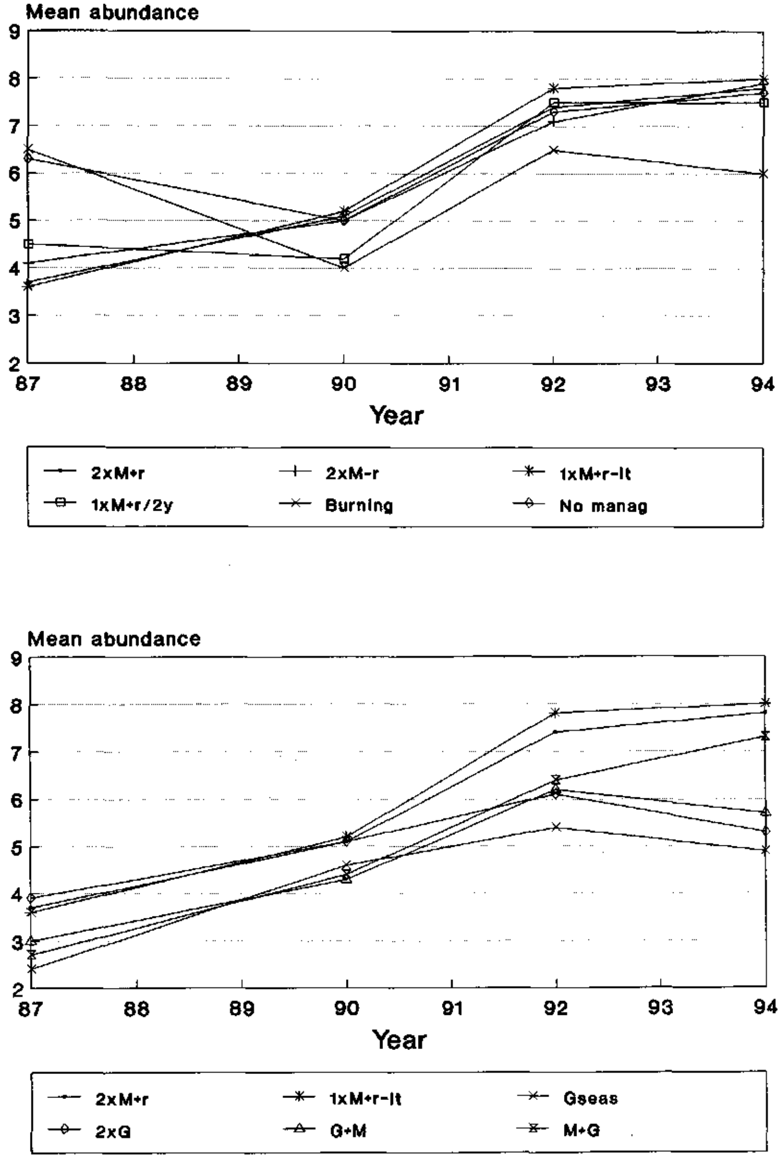
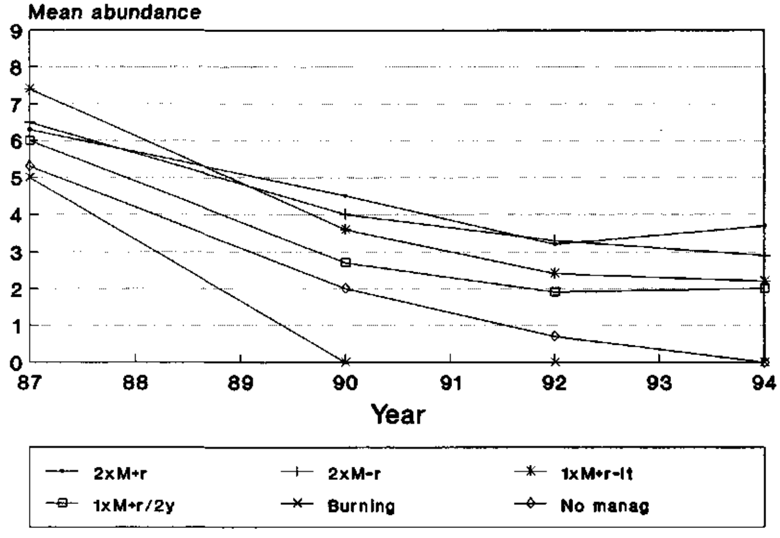


Figure 17. Mean abundance of Arrhenatherum elatius under various management strategies.

Lolium perenne was favoured by grazing practices, whereas *Arrhenatherum elatius* was favoured by mowing (see figure 18). Grazing throughout the summer led to the highest abundance of *Lolium perenne* but to the lowest abundance of *Arrhenatherum elatius*. Under burning and under no management *Lolium perenne* had disappeared in 1994.



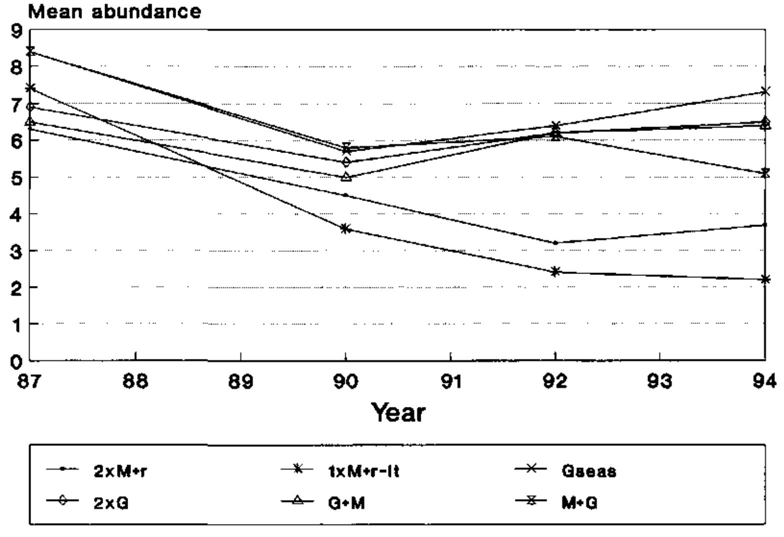
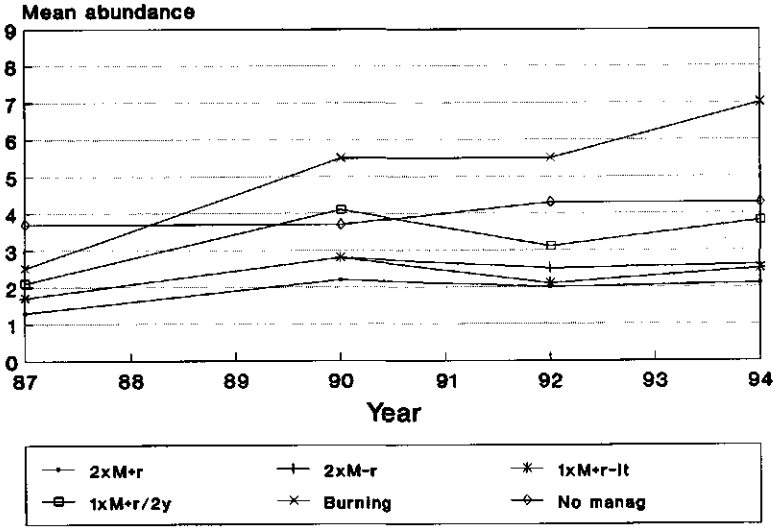


Figure 18. Mean abundance of Lolium perenne under various management strategies.

Cirsium arvense was favoured by the relatively extensive management practices burning and mowing once every two years and by no management (see figure 19). It was also slightly favoured by the grazing practices.



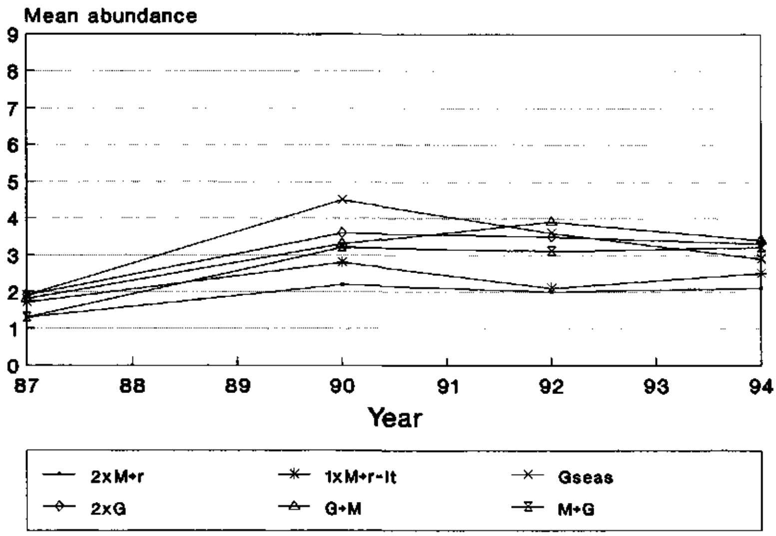
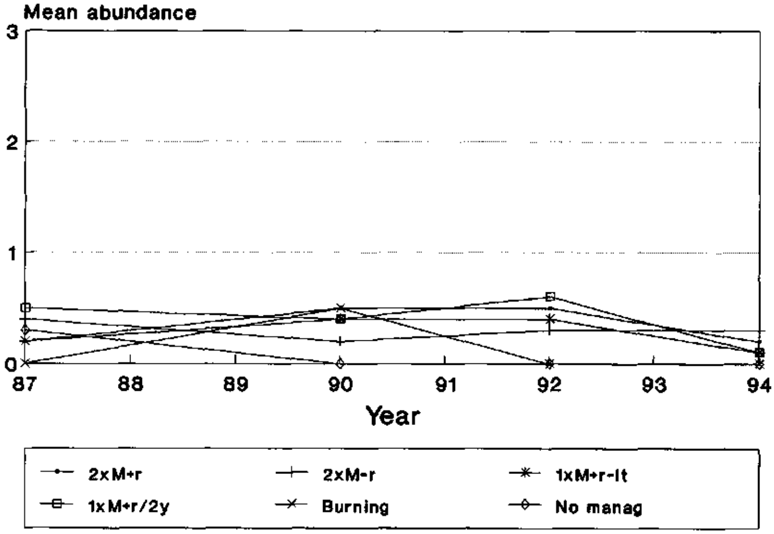


Figure 19. Mean abundance of Cirsium arvense under various management strategies.

Cirsium vulgare was favoured only by the grazing practices, especially by grazing throughout the summer, grazing twice a year and grazing in June in combination with hay-making in September (see figure 20).



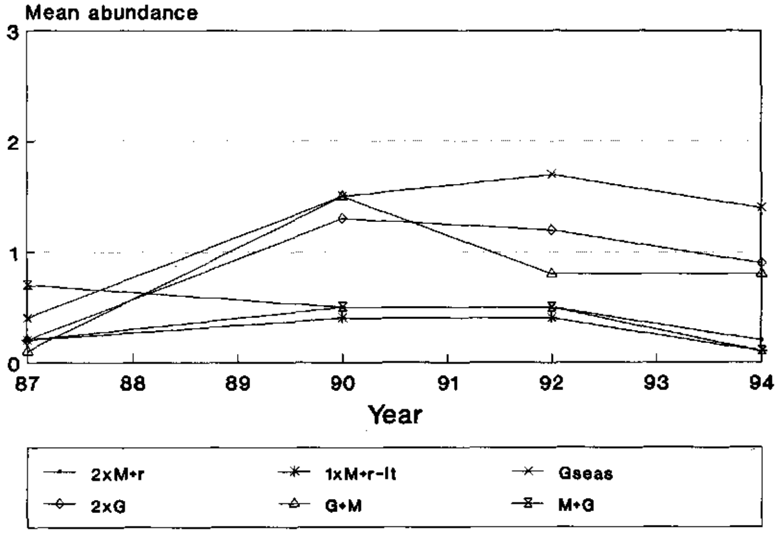
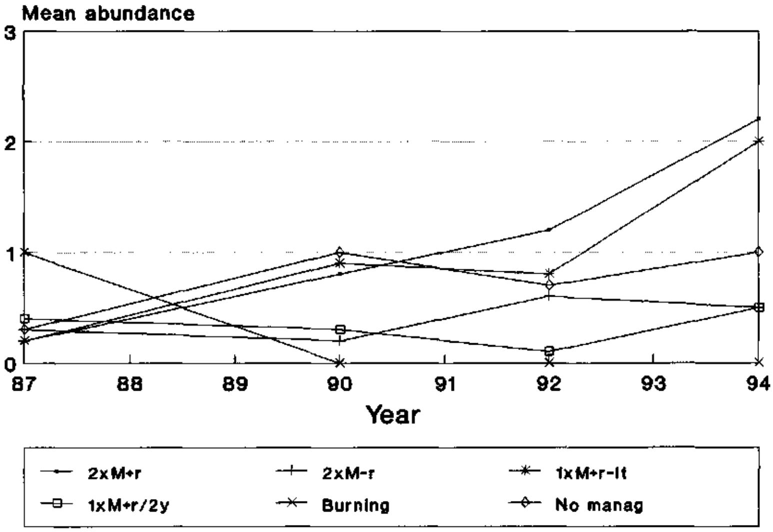


Figure 20. Mean abundance of Cirsium vulgare under various management strategies.

Crepis biennis was favoured by hay-making twice a year and hay-making once a year in September (see figure 21). Grazing througout the summer and grazing in spring in combination with hay-making in September led to an almost complete disappearance of the species.



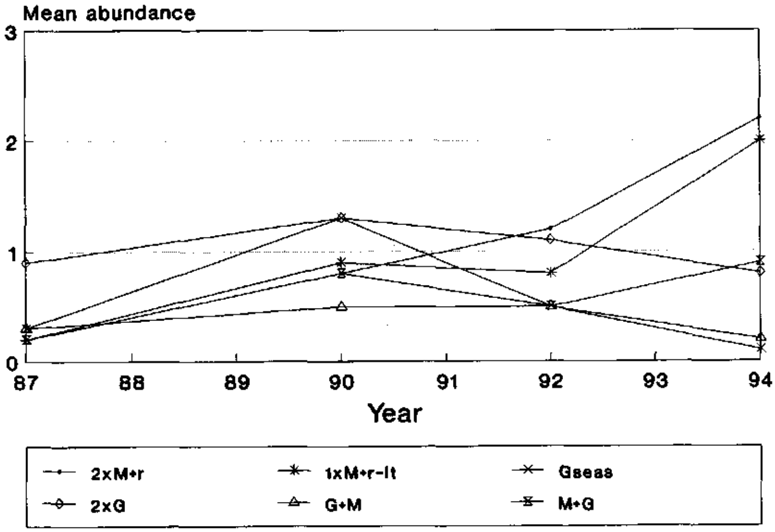


Figure 21. Mean abundance of Crepis biennis under various management strategies.

In contrast to *Crepis biennis*, *Crepis capillaris* was favoured by the four grazing practices, in particular grazing in spring in combination with hay-making in September and grazing througout the summer (see figure 22). The mowing practices led to a sharp decrease.

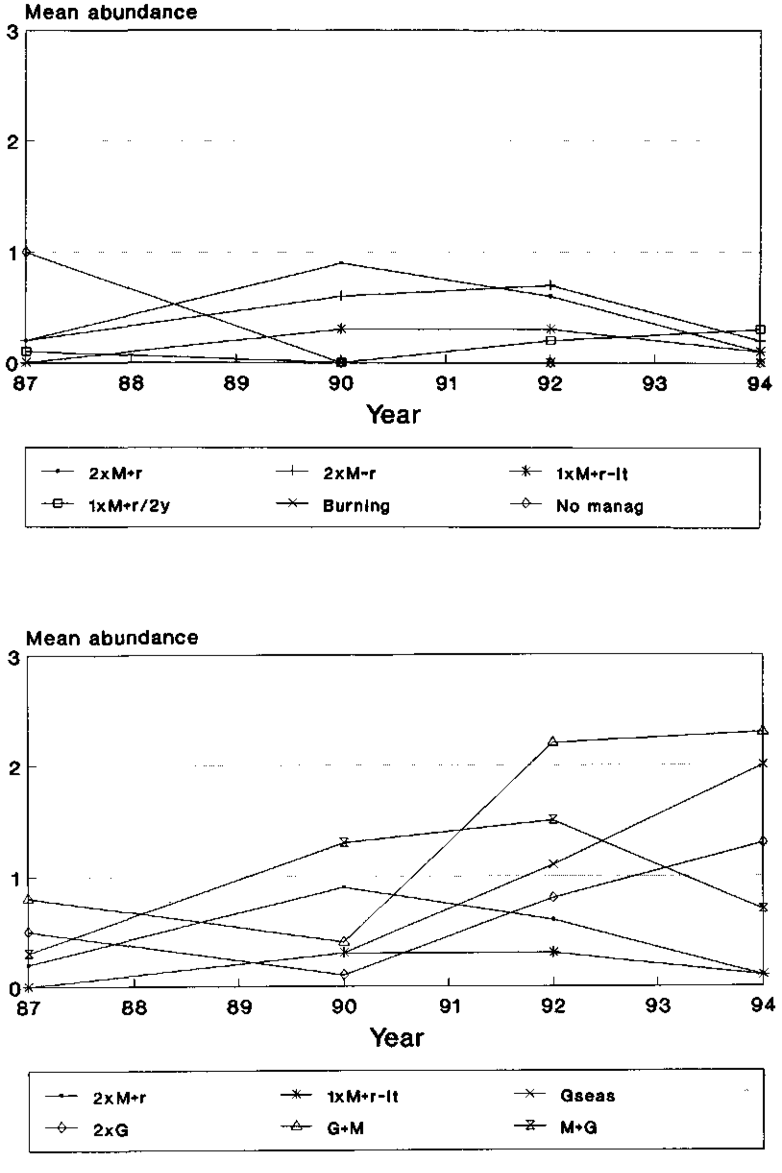
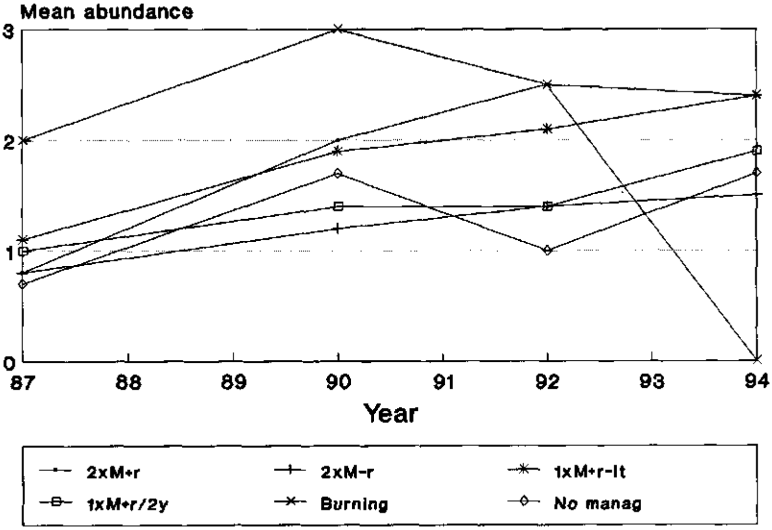


Figure 22. Mean abundance of Crepis capillaris under various management strategies.

Centaurea jacea was favoured in particular by hay-making twice a year and hay-making once a year in September but also by hay-making in June in combination with grazing in September (see figure 23).



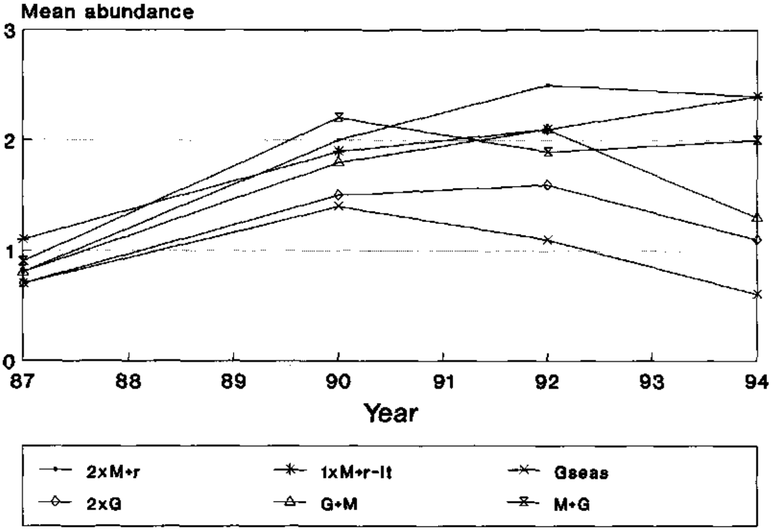


Figure 23. Mean abundance of Centaurea jacea under various management strategies.

4.4 DISCUSSION

The river dikes belong to the semi-natural landscape (Westhoff, 1952). Like other semi-natural landscapes in the Netherlands such as meadows, dune grasslands, reed swamps and heaths, they are man-made natural ecosystems, their presence being the result of a very regular, continued management. This human activity in most cases entailed periodically removing the vegetation by mowing, burning, cutting sods or grazing, and it has gone on for centuries, sometimes even for many centuries, in the same way (Sýkora & Sýkora-Hendriks, 1977; Sýkora *et al.*, 1990). It can therefore be concluded that management probably plays an important role when developing 'new' species-rich meadows on reconstructed river dikes.

The results presented in this chapter clearly show that the differences in vegetation composition and diversity in the first four years after the reconstruction were mainly caused by the different methods of reconstruction. In accordance with Tilman (1985, 1988), in the early successional stage the competition for nutrients will have been more important than competition for light, especially on the replaced topsoil and subsoil and on imported clay. In this stage the productivity was still relatively low and the sward was still quite open and there was no lack of light. After 1990 the vegetation closed and the biomass increased. This increased biomass intercepted more light, and thereby reduced light availability at the soil surface (Olff *et al.*, 1993). As a consequence, during the later successional stages competition for light became more important than competition for nutrients. As the management influences the biomass production and also the canopy structure, the impact of the management on the vegetation composition and diversity increased after 1990.

4.4.1 Plant communities

In the first few years after the reconstruction there was a large variation in the proportion of the annual and biennial pionieer species. In all methods of reconstruction these pioneer species decreased rapidly and almost disappeared. In 1990, four years after the reconstruction, differences in vegetation composition were still related to the differences in method of reconstruction (Liebrand, 1993a). In 1994, eight years after the reconstruction, the best developed community *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) still only occurred in the section with the spared zone. In this section it appeared mostly in the spared zone, but also in some permanent plots on replaced topsoil and on imported clay. These plots were always bordering the spared zone. This implies that species dispersed from the spared zone to the bordering replaced topsoil and imported clay. It seems that the chemical and physical composition of the replaced topsoil and the imported clay were suitable for the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I). The proximity of the spared zone was probably crucial as a seed source.

The species-poor *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) appeared in 1990. In that year it only occurred on replaced sods and replaced topsoil. In 1992 this community also occurred on imported clay. Until 1994 the species-rich *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) only occurred on replaced sods and replaced topsoil. In 1994 this community also appeared on imported clay, but only on imported clay bordering the replaced sods. This implies that species dispersed from the replaced complete sods to the imported clay. Again the presence of a seed source, this time in the form of complete sods, appeared to be important.

The *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV) appeared only sporadically and had almost disappeared by 1994. The *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) appeared in all methods of reconstruction. The *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) and the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) appeared in all methods of reconstruction, except on replaced sods. Community VII had almost disappeared by 1994. Communities IV and VII represent early successional stages. In 1994 community IV occurred in only 2 permanent plots, community VII in only 3 plots. The pioneer stages, the fragmentary community with *Matricaria maritima* and *Plan-*

tago major [Arrhenatherion/Chenopodion] (VIII) and the fragment community with *Capsella bursa-pastoris* and *Poa annua [Eu-Polygono-Chenopodion]* (IX) already disappeared in 1990.

4.4.2 Methods of reconstruction

Plant communities

Logically, the vegetation in the spared zone most closely resembled the vegetation that grew on the dike before the reconstruction. In two or three years just before the reconstruction the vegetation was managed badly, which probably has led to a certain fall in the number of species. It seems probable that the species richness of the original vegetation was higher than it was in the spared zone after the reconstruction. During this study the species richness on the spared zone under hay-making twice a year increased from 33 in 1987 to 49 in 1994. Under hay-making in September it only increased from 37 to 40, under hay-making once every two years from 33 to 34 and under mulching it decreased from 33 in 1987 to 31 in 1994. It is expected that optimal management will lead to a further increase of the species richness in the future because of the favourable conditions of the spared zone (i.e. optimal exposition, inclination and soil composition). From the beginning of the experiment a small number of permanent plots on replaced topsoil and on imported clay belonged to the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I). All these plots bordered the spared zone. This implies that species disperse from the spared zone to the imported clay. Clearly the chemical and physical composition of the imported clay is suitable for the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I).

Immediately after the reconstruction the species composition of the replaced complete sods showed the greatest similarity to the vegetation in the spared zone, followed by the replaced topsoil. The imported clay was least similar to the vegetation in the spared zone, followed by the replaced subsoil. Whether the vegetation in all methods of reconstruction will develop to the vegetation of the spared zone depends in the first place on the composition of the soil (Sýkora & Liebrand, 1987; van der Zee, 1992). If the soil differs in physical and chemical attributes, it is obvious that the vegetation will never become identical to the vegetation in the spared zone. The slope and the aspect will also determine the development of the vegetation (Aperdannier, 1959; van Heerden, 1979). In 1987 the vegetation in the four permanent plots on replaced complete sods belonged to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). In 1994 three of the four plots belonged to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II), whereas only the plot with management hay-making twice a year belonged to vegetation type III. This shows the importance of the management after the reconstruction. If management is wrong, this relatively expensive method of reconstruction will be wasted labour because most of the species will still disappear. Many of the experiences mentioned in the literature concerning the (re-)introduction of species in nature reserves involve the transplantation of adult individuals. Sometimes direct transplantation took place but more often seeds were collected and grown to plants in the greenhouse or experimental garden before planting out. Transplanting has been successful for many species (Glitz, 1980; Ebel & Rauschert, 1982; Wells, 1983). Although some species did not survive, a large number of species transplanted in complete sods established and spread after the transplantation (Rawes & Welch, 1972; Wathern & Gilbert, 1978). However, Londo (1984) has given examples of transplantations of some rare species that failed.

Vegetation development was most spectacular on the replaced topsoil. In 1987 most of the permanent plots on replaced topsoil belonged to the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) (44%) and the *Arrhenatheretum* with *Crepis capillaris* and *Ranunculus repens* (VI) (24%). In contrast, in 1994 the majority of the 96 plots on topsoil belonged to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) (34%), the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) (24%) and the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) (22%), which only appeared in 1990. In 1994 the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) disappeared on replaced topsoil. The development to the relatively species-rich community III in particular shows the importance of the replacement of the topsoil. The *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) only appeared on topsoil in sections C, D1, D2 and E1. In 1987 this vegetation type was already found only in section D2. In sections C, D1 and E1 it appeared in 1990. There was a striking sharp decrease of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) in section C. In this section the clay content is markedly higher (38%) than in D1, D2 and E1 where is was respectively 32%, 24% and 29%. The *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) is only able to survive on such clayey soil if the management is optimal (i.e. mowing twice a year with removal of the hay) (see also § 4.4.4). Throughout the monitoring period a small number of plots on topsoil belonged to the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I). All these plots bordered the spared zone, which suggests that species disperse from that zone to the replaced topsoil. Clearly the chemical and physical composition of the replaced topsoil was suitable for the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I).

The vegetation development on replaced subsoil was very slow. In 1994 most of the permanent plots on subsoil (61%) belonged to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) and 39% to the *Arrhenatheretum* with *Crepis capillaris* and *Ranunculus repens* (VI).

In 1987 most of the permanent plots on imported clay belonged to the association fragment community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) and the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) (52% and 43% respectively). Whereas the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) was not even present in 1987, in 1994 most of the plots on imported clay belonged to this plant community (54%). In 1994 5% of the plots still belonged to community VII which represents an early successional stage. In 1994 three permanent plots on imported clay developed to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). All plots were situated directly below the sods replaced manually. Except for the plots bordering the spared zone, the development in 1994 in the permanent plots on imported clay was not as advanced as it was directly below the sods replaced manually. This implies that the proximity of the sods replaced manually was crucial.

Species richness

In general the mean species richness decreased between 1987 and 1990 and increased between 1990 and 1994. In 1987 species richness of imported clay was significantly lower than of all other methods of reconstruction. In 1990 the species richness of imported clay was only significantly lower than of complete sods and topsoil and in 1992 it was significantly lower than that of the subsoil, spared zone and topsoil. In 1994 the species richness in the spared zone and on replaced subsoil was significantly higher than on imported clay and complete sods. The mean species richness on replaced topsoil was intermediate.

In 1987 species richness was highest on the complete sods thanks to the favourable site conditions (i.e. exposition and inclination) and an optimal management before the transplantation. In 1994 the mean species richness over the four trial plots was lowest here. The clay content of the complete sods was significantly higher than of all other methods of reconstruction (see chapter 5). This relatively high clay content in combination with less favourable management in three of the four trial plots brought about a high biomass production and consequently a relatively low species richness (see also chapter 5).

The mean number of grass species on the imported clay was significantly lower than on the other methods of reconstruction. In the spared zone, on replaced topsoil and on replaced subsoil the mean number of herbs was significantly higher than on sods and on imported clay. In 1987 the sequence of the methods of reconstruction in terms of decreasing number of species was: complete sods > spared zone > replaced topsoil > replaced subsoil > imported clay. In 1994 this sequence was: spared zone > replaced subsoil > replaced topsoil > imported clay > complete sods. Obviously the higher species richness on replaced subsoil compared to replaced topsoil was promoted by the relatively favourable soil composition (i.e. low lutum and high sand content, low N content and low N mineralization, see chapter 5).

4.4.3 Sowing

Plant communities

The spared zone and the replaced complete sods were not seeded at all. All the permanent plots on replaced topsoil and imported clay that belonged to the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) bordered the spared zone and all the permanent plots on imported clay that belonged to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) bordered the replaced complete sods. This study shows that it is reasonable to infer that the effect of the dispersal of the species from the spared zone and the replaced complete sods to the neighbouring parts of the improved dike is more effective than seeding these parts.

On the replaced topsoil only the permanent plots sown with D1+LGM had developed to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) in 1994. In all other permanent plots the development did not go further than the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). Sowing seeds gathered locally (LGM) on topsoil appeared to accelerate the development of the vegetation. Addition of *Lolium multiflorum* did not seem to affect the development. The development of the unsown permanent plots was somewhat slower but by 1994 they had reached the same stage. Sowing with BG5 appeared to retard the vegetation development.

On subsoil 'no sowing' appeared to lead to the fastest development of the vegetation. The permanent plots sown with LGM developed somewhat slower. Addition of *Lolium multiflorum* appeared to retard the development. Sowing solely with BG5 retarded the development of the vegetation on subsoil. On imported clay sowing with D1+LGM led to the fastest development of the vegetation whereas sowing solely with D1 showed a somewhat slower development. The development of permanent plots sown with BG5 was retarded.

In a sowing experiment with *Agrostis capillaris* and *Festuca filiformis* on canal verges Zwaenepoel (1995) found that many species successfully regenerated but that the rarer and therefore often more appreciated species did not appear. In addition, he determined a switch from annual to perennial vegetation mainly within three years. The species composition of the new sown verges and old unaltered natural verges was quite different. Differences in slope were important for the differentiation of sown species as well as for differentiation in the spontaneously established vegetation. Differences in aspect were mainly important for the sown species whereas also the moisture and nutrient status of the soil played a detectable role in vegetation differentiation.

Most standard seed mixtures contain *Lolium perenne*. This fast growing grass species is able to cover reconstructed river dikes and road verges within a few months. After a while, especially under hay-making regimes without manuring, its abundance decreases and it is replaced by other grass species and herbs (Krause, 1989). On sandy nutrient-poor soils, this process is very fast (Trautmann & Lohmeyer, 1978). *Arrhenatherum elatius* only appears after the soil has developed to a stage at which sufficient nutrients become available (Krause, 1989). Krause (1989) recommends forgoing sowing seed mixtures if the newly contructed banks are so stable that they do not need a protecting grassy sward, because with the passage of time a plant cover of indigenous plants will develop. This recommendation should be seriously considered, especially for the side of the dike furthest away from the river, certainly if the topsoil containing propagules of the former vegetation has been replaced. This landward side of the river dikes is less likely to be influenced by the eroding forces of the river water and so a quick development of an erosion-resistant sward is less urgent here than on the side facing the river.

Species richness

In 1987 species richness in the D1 sowing was significantly lower than in the sowings with D1+LGM, LGM, Lm+LGM, BG5 and in 'no sowing'. Additionally 'no sowing' had significantly more species than D1+LGM and BG5+LGM. With the exception of the D1 sowing, the mean species richness decreased between 1987 and 1990 and increased between 1990 and 1994. Sowing with BG5 showed a particularly sharp decrease between 1987 and 1990. In 1990 species diversity in sowing with BG5 was significantly lower than in sowing with D1+LGM. This negative effect of sowing with

BG5 was only visible between 1987 and 1990, thus only immediately after the reconstruction. After this period species diversity increased, as it did in all other sowings. In 1992 and 1994 there were no longer any significant differences in species diversity.

4.4.4 Management

Plant communities
From 1987 to 1994 all permanent plots in the spared zone belonged to the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) irrespective of the management applied.

In 1987 all permanent plots on the replaced complete sods belonged to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). In 1994 three of the four plots belonged to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II). The management of these plots was mulching twice a year, hay-making in September and hay-making once every two years. In 1994 only the plot with the management hay-making twice a year still belonged to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). There were no grazed plots on the replaced sods. It has already been noted that the clay content of the complete sods was significantly higher than of all other methods of reconstruction (see chapter 5) and that this relatively high clay content caused the high biomass production. The relatively large proportion of ruderal species and the low species richness (see also chapter 5) are also ascribable to the high clay content. Apparently, only the most frequent management with removal of the mowings was able to prevent the species-rich community III developing to the species-poor community II.

In 1987 most of the permanent plots on replaced topsoil belonged to the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII). Hay-making twice a year and hay-making in June in combination with mulching in September encouraged a development to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) (47% and 67% respectively). None of the plots under those management practices developed to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II). Plots which were mulched twice a year without removing the mowings also developed to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) (33%) but also to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) (25%). Hay-making once a year gave nearly similar results regardless of whether the mowing was in June or in September. At both management practices a part of the plots developed to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) (29% and 23% respectively). Most of the plots with hay-making once every two years in September developed to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) (55%). In 1994 many plots that had only been grazed developed from the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) (Gseas: 40%, 2xG: 50%). Only a few grazed plots developed to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). None of the grazed plots developed to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II). In 1994 the burned plots and the plots without management all developed to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II).

In 1987 all permanent plots on former subsoil belonged to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) and the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII). In 1994 all mown plots developed to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) and all grazed plots belonged to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI).

In 1987 all permanent plots on imported clay, except for one, belonged to the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) and the fragment community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII). In 1994 the mown plots had developed mainly to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) whereas the grazed plots developed mainly to the *Lolio-Cynosuretum* with

Crepis capillaris and *Ranunculus repens* (VI). The unmanaged plot developed from the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). All permanent plots on topsoil and on imported clay belonging to the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) bordered the spared zone. The vegetation development of these plots was probably not due to the presence of propagules in the soil but to the dispersion of the propagules from the spared zone to these plots. All three permanent plots on imported clay that in 1994 belonged to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) bordered plots with replaced sods. It seems likely that their development was aided by the immigration of the propagules from the replaced sods. On subsoil and on imported clay the development of the vegetation was slower than on replaced topsoil, in spite of the management. This underlines the importance of the presence of propagules in the soil used.

Ignoring the method of reconstruction
In 1987 most of the permanent plots belonged to the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII), in spite of the management. In 1994 most mown plots belonged to the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) whereas most grazed plots belonged to the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI), except for those with hay-making in June and grazing in September. All the plots that still belonged to the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) in 1994 were grazed. In 1994 16% of the mown plots belonged to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) and 7% of the grazed plots. Whereas mowing seems to encourage the development from the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III), grazing seems to prevent it. The proportion of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) was relatively high under hay-making twice a year (24%) and under hay-making in June in combination with mulching in September (20%). In 1994 15% of the mown plots belonged to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II), whereas not one grazed plot developed to community II. The proportion of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) was relatively high in the mowing once every two years in September and removing the mowings treatment (33%) but also under mowing twice a year without removal of the hay (21%) and under mowing once a year in June with removal of the hay (22%). The plots burned in February and 2 of the 3 unmanaged plots developed to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) in 1994.

The *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) was only found under mowing regimes. None of the pastures contained a spared zone. Therefore on the basis of this research it is not possible to say whether community I can also occur under grazing practices. On the other hand, many species of this community are typical for hay-making management and most of them are expected to be intolerant of high grazing pressure (Van Gils *et al.*, 1975). So it is unlikely that community I is able to develop in pastures.

Species richness
With the exception of burning and 'no management' the species richness of the management practices did not differ very much in 1987. The relatively high numbers of species in the burned and unmanaged plots in 1987 were due to the great amount of disturbance. There were numerous annual pioneer species in these two treatments. Apart from burning and no management all other management practices showed an increase in the species richness between 1987 and 1994. Significant differences appeared only after 1990. In 1992 species richness under hay-making twice a year was significantly higher than in most other management practices. In 1994 species richness under hay-making twice a year was significantly higher than of hay-making once every two years, mulching twice a year, grazing twice a year, grazing in June in combination with hay-making in September, grazing throughout the summer, burning and no management. The species richness of hay-making in

June in combination with grazing in September, hay-making once a year, either in June or in September, and hay-making in June in combination with mulching in September was intermediate. This suggests that vegetation change can be manipulated by management, even under the unfavourable situation of long and narrow embankments (unfavourable area/perimeter ratio) bordering intensively used arable land. Of course in this case dispersion problems should be taken into account.

In a study of the population structure of *Gentiana pneumonanthe* Oostermeijer *et al.* (1994) distinguished three different population types: (a) 'invasive' or 'dynamic' populations, characterized by high densities of seedlings and juveniles relative to the adult age states, (b) 'normal' or 'stable' populations with adult age states prevailing, but with low densities of seedlings and juveniles, and (c) 'regressive' or 'senile' populations, consisting exclusively of adult flowering and adult vegetative individuals. Analogous to this progression, on reconstructed river dikes a clear trend can be observed in the age state structure, from 'invasive' populations in young successsional stages to 'normal' populations in relatively stable situations under hay-making management and relatively extensive grazing regimes. Mulching management which brings about a litter layer, intensive grazing which causes a continuous stress, burning of the vegetation and no management at all lead to domination of grasses or shrubs and therefore to a 'regressive' population structure.

Hay-making once or twice a year

In this study mowing with removal of the mowings (i.e. hay-making) twice a year resulted in an increase of the species diversity and in the highest number of species of all management practices in 1994. This is in agreement with the results of many other studies. In a study of the long-term effects of several cutting treatments on roadside vegetation Parr & Way (1988) found the highest species richness in plots cut twice per year and the lowest species richness in the uncut plots. In their study, increased cutting frequency significantly decreased the species frequency, mainly of a number of coarse species including *Elymus repens*, *Arrhenatherum elatius* and *Anthriscus sylvestris*. Many finer species (mostly grasses) increased in frequency. They also found that removing the mowings led to an increase in species richness, mainly due to an increase in herbs.

Hay-making once a year in June or September resulted in a small increase in the number of species. According to Sýkora *et al.* (1990) on soils with a relatively high nutrient status mowing once a year is insufficient, since such sites appear to ruderalize. This is in accordance with Bakker & De Vries (1985) who suggested that on nutrient-rich soils species-rich hay meadows can only develop when mown twice a year. Nevertheless, Bakker (1989) found a stabilization or an increase of the species diversity as result of mowing only once a year. Additionally he suggested that the timing of the mowing is important. In a relatively low-productive grassland (4 ton dw.ha^{-1}) the site which is cut in September contains more species than that cut in July, whereas the reverse is true in a high-productive grassland (8 ton dw.ha^{-1}). A large standing crop in the summer period apparently hampers many species. In their study in an *Arrhenatherion elatioris* vegetation Oomes & Mooi (1981) concluded that some lower-growing species only persisted or spread in the June mowing regime whereas some tall-growing species increased remarkably with September hay-making. Krüsi (1981) found the June hay-making regime to be advantageous for medium-sized species in *Mesobrometum* communities but unfavourable for tall-growing species. Egloff (1986) also found that in *Molinion* communities tall forbs were favoured more by September cut than by cuts in June or July. From these results Bakker (1989) concluded that late cutting regimes differ from earlier cutting regimes by encouraging tall-growing species. However, at the conclusion of the present study no such differentiation was yet visible.

In the present study hay-making every second year in September resulted in a small increase in the number of species. This is in contrast to the findings of Bakker (1989) who found decreasing species diversity in most of the communities studied.

The time and frequency of cutting may be related to the growth of important species in the sward, in order to control dominant and aggressive grass species at the peak of growth or to allow rare plant species to complete their life cycle. To survive, plant species must be able to produce seed occasionally (Duffey *et al.*, 1974; Grootjans, 1980; Oomes & Mooi, 1985). In the light of this, the management after a river dike reconstruction should primarly consist of restoration management and secondarily of continuation or maintenance management. The restoration management should be directed at the control of the dominant and aggressive grass species by affecting them at the peak of growth by mowing or intensive grazing. The continuation or maintenance management should be aimed at allowing rare plant species to complete their life cycle.

Hay-making in combination with grazing
In this study hay-making in June in combination with grazing in September resulted in an increase of the species diversity and the second highest number of species of all management practices in 1994. In this management the biomass production is reduced by hay-making and removal of nutrients in June which encourages a high species richness. In autumn, germination gaps are created by livestock grazing at that time (Smith & Rushton, 1994). After a short period of relatively intensive grazing the livestock are removed which subsequently allows an optimal growth of seedlings of autumn-germinating species and established plants, additionally favoured by the lack of spring grazing in the next year. Grazing in June in combination with hay-making in September resulted in a stabilization of the species diversity. As it is for hay-making once a year, the timing of the mowing might also be important in these combined management practices. A relatively low-productive grassland which is grazed in June and cut in September might contain more species than one cut in June and grazed in September, whereas the reverse is true in a high-productive grassland. Again, a large standing crop in the summer period apparently hampers many species (Bakker, 1989).

Sýkora *et al.* (1990) found that hay meadows varying from species-rich to species-poor did not show any change when mown in summer followed by light grazing of the regrowth. This suggests that although mowing once in summer is insufficient for the maintenance of hay meadows, light grazing of the regrowth contributes to their stabilization. If after mowing the grazing is more intensive, the vegetation will most probably improve. It will deruderalize and species diversity will increase.

Grazing
Both grazing twice a year and extensive grazing throughout the summer resulted in a stabilization of the species diversity. In 1994 the number of species under extensive grazing throughout the summer was second lowest of all management practices.

Sýkora *et al.* (1990) showed that the highest intensities of grazing by a flock of sheep (i.e. between 8 and more than 15 hours a month by 200 sheep per 500 m of embankment) were best suited for the improvement or maintenance of the conservation value of the vegetation on embankments in the Zak of Zuid-Beveland. Under the same conditions, light grazing (less than 8 hours) proved to be insufficient and enabled communities with less conservation value to develop. At low sheep densities, the more palatable species will be heavily grazed, while other herbage will be avoided. This leads to patchiness in the vegetation structure. At higher sheep densities the less palatable plants will also be grazed (Duffey *et al.*, 1974). With more intensive management, species of high competitive index are suppressed and conditions favourable to less aggressive species prevail (Grime, 1973). Sheep control the dominant grasses and allow shorter herbs to thrive. Grazing at the time when the dominant grasses are making their maximum growth (mid-May to mid-June) is an effective way of controlling competitive ability, especially when the stocking density is relatively high (Sýkora *et al.*, 1990). Duffey *et al.* (1974) used 24 sheep per ha on chalk grassland for a short period.

The relative abundance of the species is largely determined by the frequency and timing of grazing and by the frequency of establishing of different species from seed (Mitchley & Grubb, 1986). Many seeds are dispersed by becoming attached to the fleece of the sheep (Hillegers, 1985).

In a study of the effects of grazing management regimes Smith & Rushton (1994) found that vegetation changes were related to the grazing regime and to the time of grazing. Changes in the species composition of the plots were associated with species' strategies (*sensu* Grime, 1979) in the established and regenerative phases. O'Connor & Pickett (1992) also found that variation in species composition reflected grazing history. Lightly grazed sites were characterized by longer-lived palatable perennials and heavily grazed sites by shorter-lived perennials, unpalatable species and some forb species. In a study of the effects of sheep grazing on the vegetation change in a species-poor grassland and the role of seedling recruitment into gaps Bullock *et al.* (1994a) found that the dicots exhibited stronger and more consistent responses to grazing than the grasses. The abundance and the species number of the dicot species were significantly increased by increased grazing in one or more grazing periods. Intensive grazing appeared to create gaps in the vegetation in which seedlings were able to establish. There appeared to be no evidence of a persistent seed bank, so all seeds were probably derived from recent seed rain. No species novel to the vegetation emerged in the gaps. Because of the small responses of the grasses to the grazing treatments and the lack of input of novel species from a seed bank or seed rain they concluded that vegetation change is likely to be slow, especially while fertility is high. However, they conjectured that the dicots may continue to increase under increased grazing because of their high seed production and the effects of grazing in increasing gap frequencies. Gibson & Brown (1992) suggested that, irrespective of grazing treatment and local conditions, secondary succession from arable land towards species-rich calcicolous grassland appears to take at least a century to run its course. Thus, grazed grassland and forest successions can operate over similar time-scales.

From the wildlife point of view, grazing is more satisfactory than mowing because it creates a series of plant micro-habitats within the sward, which may provide niches for germination and growth which are not available in mown grasslands (Wells, 1980; Bakker & Ruyter, 1981). Grazing animals tend to return to formerly closely grazed swards to graze protein-rich young tillers and avoid rugged areas, thus reinforcing structural differences in the vegetation. In this way both alpha- and beta-diversity may increase (Bakker & Ruyter, 1981; Bakker *et al.*, 1984, Bakker, 1987a). Well developed micro-habitats mainly occur on larger areas. The area of river dike grasslands is mostly too small to create well functioning micro-habitats with their accessory flora and fauna.

Sýkora *et al.* (1990) found that under the influence of light cattle grazing on embankments, hay meadows turned into species-rich pastures. Cattle tend to be less selective than sheep and, because of this, often create a grassland which consists of a mosaic of short turf interspersed with taller patches (Klapp, 1971; Wells, 1980). Vegetation fouled by dung will not be grazed for 12-20 months (Kydd, 1964). Continuous and close rotational cattle grazing may result in a sward with a high proportion of forbs (Wells, 1970). To date, Dutch river dikes have been mainly grazed by sheep which are hardly able to create micro-habitats. One option for the grazing of river dikes is to use heifers up to 18 months old. Under dry conditions the weight of these animals is acceptable for the slopes of river dikes. The sward is not damaged by their trampling.

Vegetation development under grazing management depends on periods of respite from grazing during which plants can flower and spread seeds, thus enabling rejuvenation of the vegetation. Many plant species that are never given the opportunity to flower will die out after some time. So relatively intensive grazing throughout the summer will ultimately lead to a species-poor vegetation.

Mulching or mowing without removing the mowings

In terms of ecosystem dynamics there is difference between mulching and not removing the mowings. Mulching implies finely shredded material whereas in this study the mowings were left as a swathe. Shredded material breaks down more rapidly.

In this study mowing without removal of the mowings led to the largest above-ground biomass and to the least species richness of all mowing regimes. In productive habitats strong competition for light favours the tallest species (Newman, 1973). Additionally, in productive grasslands species richness is low because accumulated litter, and possibly lower light penetration, inhibit germination and survival of seedlings (Tilman, 1993). Carson & Peterson (1990) found that in an old field removal of litter significantly increased seedling densities, and addition of litter decreased seedling densities and species richness. Bakker (1989) found a decrease of number of species in almost all communities with a mulching management. In contrast, other studies have shown an increase in species diversity under this management (Schiefer, 1981, 1983; Schreiber & Schiefer, 1985). Bakker

(1989) surmises that this is probably because in these studies no litter accumulation was observed, despite mulching. It was apparently mineralized quickly because of the relatively high autumn temperatures in southern Germany. Only if mulching was done later than mid-August, litter did persist until the early summer of the following year.

Burning
In the present study the species richness decreased sharply under the burning management. In 1994, the management regime with the least species richness was burning. Additionally, burning of the vegetation resulted in considerable ruderalization. Both the standing material and the litter layer were burned in the study area; this caused a large quantity of plant nutrients formerly immobilized in plants and litter to be released to the soil (Duffey *et al.*, 1974). So, burning prevented litter accumulation. Although N and S are volatilized in the combustion of plant tissue, all other nutrients are changed into simple salts that are water-soluble and hence immediately available for regrowth of the vegetation (Daubenmire, 1968). Peak standing crop is often found to be largest on burned sites, which may have low species diversity. From the results of diverging plant communities Schreiber (1980) and Schiefer (1982) concluded that winter burning alone could not prevent the vegetation from succeeding along the direction similar to that of the no management practice or abandonment. Not only do the changes proceed much slower, but small species, especially stolon and rosette hemicryptophytes, disappear in favour of tall-growing species with rhizomes and below-ground tillers. Therefore, controlled burning alone cannot maintain semi-natural grassland communities. It must be combined with a hay-making or mulching regime (Schiefer, 1981). Sýkora and Sýkora-Hendriks (1977) concluded that the burning of dikes causes a vigorous growth of tall forb communities; the availability of nitrogen and phosphorus for plant growth is enhanced by burning, while at the same time species such as *Rubus caesius*, *Rosa canina* and *Crataegus monogyna* can cope with these fires, which have their major effect on the forb layer.

No management or abandonment
The cessation of all agricultural practices or management activities results in an increase of above-ground biomass, an increased growth of grasses, a considerable accumulation of litter and in a decrease in species number and a dominance of a few species only (Wells, 1970; van der Maarel, 1971; Willems, 1983; Hillegers, 1984). On abandoned grasslands the number of species is low, only little light is transmitted by the dominant tall forbs and 80-90% of the soil is covered with litter (Bakker & de Vries, 1985). Nearly all the studies that have compared different management practices show a decreased number of species after 5-10 years of abandonment. This is in agreement with the results of the present study, although in 1994 the number of species showed a small increase. In 1994 the shrub *Rubus caesius* was very abundant and some seedlings of *Crataegus monogyna* were also found. Ellenberg (1978) suggested a diverging development on an abandoned pasture and meadow. Shrubs were already present in these pastures because of marginal agricultural use prior to abandoning. Former pastures can, therefore, develop into woodland after three or four decades, whereas former hayfields remain without trees because they cannot emerge in the accumulated litter layer. Schreiber & Schiefer (1985) found that shrubs invaded relatively rapidly in abandoned communities with rapid litter decomposition. Hardly any tree seedling emerged in communities with a permanent litter layer or accumulation of litter during the first ten years of abandonment. They also found that tall-growing hemicryptophytes and rhizome plants proved to be able to compete and to dominate in the new set of species, strongly suppressing stolon and rosette hemicryptophytes. Stöcklin & Gisi (1985) suggest that two factors contribute to the litter accumulation in hayfields after cessation of agricultural practices: 1) dead plant material is no longer removed, and 2) a shift in species composition from easily decomposable grasses and herbs in cultivated hayfields to grasses and herbs with a higher content of cellulose and lignin in fallows favouring the accumulation of a thick layer of litter. Willems (1985) emphasized the character of the growth form of the dominant species in determining species diversity. Bakker (1989) concluded that growth forms show a more consistent successional response than do species.

With no management a 14-year period proved to be sufficient for the development of a dense scrub vegetation with a woodland character on embankments (Sýkora *et al.*, 1990). According to Duffey *et al.* (1974) on deeper, richer soils, grasslands may take about 15 years to develop to a fairly mature scrub. Knop & Reif (1982) suggested that the time needed for the development of scrub after cessation of cutting depends in the first place on the distance from the nearest scrub communities.

Sequence of management practices from good to bad

From a nature conservation point of view the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) is considered to be the best developed community (see Chapter 3). The *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) is considered to be the worst developed community. With respect to the proportions in terms of percentages of either of these communities a general trend in the sequence of the management regimes can be seen. The qualification sequence from good to bad management is as follows:

1. hay-making twice a year (2xM+r);
2. hay-making in June in combination with grazing in September (M+G);
3. hay-making in June in combination with mulching in September (2xM+-r);
4. hay-making once a year in September (1xM+r-lt);
5. hay-making once a year in June (1xM+r-el);
6. mulching twice a year (2xM-r);
7. hay-making once every two years in September (1xM+r/2y);
8. grazing throughout the summer season (Gseas);
9. grazing twice a year (2xG);
10. grazing in June in combination with hay-making in September (G+M);
11. no management;
12. burning of the vegetation.

With respect to a decreasing number of species the qualification sequence from good to bad management is as follows: 2xM+r > M+G > 1xM+r-lt > 2xM+-r > 1xM+r-el > 1xM+r/2y > 2xM-r > 2xG > no managment > G+M > Gseas > Burning.

The qualification sequences given above can be summarized as follows:

1. Good management: 2xM+r;
2. Moderate management: M+G, 2xM+-r, 1xM+r-lt, 1xM+r-el, M+G;
3. Bad management: 2xM-r, 1xM+r/2y, 2xG, Gseas, G+M, no management, burning.

In 1987 the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) had not yet appeared. This community did not appear when mown twice a year with removal of the hay and when grazed. Bad management favoured this community. In 1994 69% of the permanent plots with community II had bad management and 31% had moderate management. In 1987 the management in 45% of the permanent plots with the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) was bad and in 55% good or moderate. In 1994 67% of the permanent plots with community III had good or moderate management and only 33% had bad management. The proportion of good management increased from 18% to 33% whereas the proportion of bad management decreased from 45% to 33%. Although the species richness decreases rapidly under bad management, the change in vegetation is somewhat slower so the shift from one to another plant community takes some time. Besides, the speed of development depends on the site conditions (i.e. soil composition, exposition and inclination). These facts might explain why still 33% of the best developed community occur under bad management practices. The proportion of grazed permanent plots in the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) decreased from 20% in 1987 to 10% in 1994. In contrast, the proportion of grazed permanent plots in the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) increased from 14% in 1987 to 58% in 1994.

Under good management the proportion of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) increased from 5% in 1987 to 24% in 1994. Under bad management the proportion of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) increased from 0% in 1987 to 32% in 1994. Under moderate management the proportion of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) increased from 0% in 1987 to 11% in 1994. On the grazed permanent plots the proportion of the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) increased sharply from 15% in 1987 to 63% in 1994.

On the basis of method of reconstruction, management and successional stage a classification of the plant communities can be made:

1. Community I: vegetation of the spared zone;
2. Community II: species-poor, rough vegetation as result of bad management;
3. Community III: species-rich grassland with good and moderate management;
4. Community V: intermediate vegetation;
5. Community VI: grazed grassland;
6. Communities IV, VII, VIII and IX: pioneer stages, wholly or nearly disappeared in 1994.

Effect of management on species dispersal from the spared zone and the replaced complete sods
In all years the vegetation in the spared zone was assigned to the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I). Additionally, a small number of permanent plots on topsoil and on imported clay also belonged to this community. These permanent plots always bordered the spared zone. This implies that species dispersed from the spared zone to the bordering replaced topsoil and imported clay. Apparently, the chemical and physical composition of the replaced topsoil and the imported clay were suitable for the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I). Only hay-making twice a year and hay-making in September appeared to stimulate the development of the vegetation of those permanent plots bordering the spared zone to community I.

In 1987 all permanent plots on the replaced sods were assigned to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). In 1994 only the vegetation under management hay-making twice a year still belonged to this community. Under all other managements the vegetation belonged to the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II). In 1994 most permanent plots on the imported clay bordering the replaced sods belonged to the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). This implies that species dispersed from the replaced complete sods to the bordering imported clay. So, whereas the vegetation on the replaced sods changed from the species-rich community III to the species-poor community II, due to inappropriate management, in the meanwhile species dispersed from the replaced sods, bringing about a change from the early successional community VII to the species-rich community III on the imported clay bordering the replaced sods.

The management practices of grazing and cutting can be implemented for nature conservation. The major aim of nature conservation is the maintenance or the creation of conditions in natural and semi-natural landscapes for as many species as possible and, in particular, for those which are rare or endangered (Bakker, 1989). The various practices implemented are 1) restoration management and 2) maintenance management. Immediately after a dike reconstruction the management should be aimed at creating optimal conditions for a successful development of a species-rich vegetation with rare and endangered species whereas after some years the management should be aimed at the maintenance of this vegetation. The length of the period of the restoration management is determined by the method of reconstruction that has been applied. Sparing a zone of the former vegetation, replacing complete sods and replacing the former topsoil which contains propagules of the former vegetation stimulate a relatively fast development of a species-rich vegetation. In these situations the switch from restoration to maintenance management can be made after three or four years. When the former subsoil is replaced as the new topsoil or when the new topsoil consists of imported clay not containing any propagules the vegetation develops much more slowly.

Effect of management on individual species
Arrhenatherum elatius and *Lolium perenne* were the two most prominent grass species. *Arrhenatherum elatius* was favoured by mowing practices, whereas *Lolium perenne* was favoured by grazing. Grazing throughout the summer led to the lowest abundance of *Arrhenatherum elatius* but to the highest abundance of *Lolium perenne*. Under burning and under no management *Lolium perenne* had disappeared in 1994. *Arrhenatherum elatius* is a pronounced hayfield species. In contrast with the suggestions of Kruijne *et al.* (1967), Elberse *et al.* (1982) found that a high soil pH is not necessary for this species. Under high fertility and low pH *Arrhenatherum elatius* persists for a long period, but will ultimately be suppressed by *Holcus lanatus* (Williams, 1978). *Lolium perenne* is a pronounced pasture species, which dwindles rapidly and almost disappears if grazing is replaced by hay management (Elberse *et al.*, 1982). In fertilized and limed pasture plots it spreads rapidly, but it persists at a consistent level in unfertilized pasture plots. According to Kruijne *et al.* (1967) this species is especially common in pure pastures that are very fertile.

Cirsium arvense was favoured by the relatively extensive management practices burning and mowing once every two years and by no management. It was also slightly favoured by the grazing practices. *Cirsium vulgare* was favoured only by the grazing practices, especially by grazing throughout the summer and by grazing twice a year. In a grazing experiment to study the demography of *Cirsium vulgare* Bullock et al. (1994b) found that more intense summer or winter grazing increased seedling emergence by increasing the proportion of microsites with no canopy or with no litter. Seedling survival was increased by winter or spring grazing and winter grazing increased the year-to-year survival of the rosettes. These effects probably occurred through selective grazing decreasing competition from the dominant grasses.

Some species which occur on embankments, for instance *Origanum vulgare*, are known to increase after reducing the frequency or even ceasing the mowing (Zimmerman, 1979). Species occurring on the experimental river dike which show more or less the same reaction to a decrease of frequency or the cessation of mowing are *Agrimonia eupatoria*, *Cruciata laevipes*, *Senecio erucifolius*, *Verbascum nigrum*, which are all assigned to the alliance *Trifolion medii* of the class *Trifolio-Geranietea sanguinea* (Westhoff & Den Held, 1969). This plant community usually occurs under irregular and/or infrequent management.

4.4.5 Above-ground biomass

Between 1987 and 1994 the biomass production increased in most plots. In 1990, 3 years after the reconstruction, the peak standing crops of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) and the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) were already significantly larger than of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III), the *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV), the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) and the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII).

In 1994 the differences in peak standing crop further increased. In that year the peak standing crops of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) and the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) were again significantly smaller than of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) and the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). The mean species richness ranged from 46 in community III with biomass 5.9 ton dw.ha^{-1} to 29 in community II with biomass 8.3 ton dw.ha^{-1} (dw = dry weight). There appears to be a negative correlation between the above-ground biomass and the species richness (see also chapter 5).

Except in extremely infertile grasslands, the number of species decreases with increasing biomass production (Marschall, 1966; Thurston, 1969; Rorison, 1970; Van der Maarel, 1971; Dirven & Neuteboom, 1975; Silvertown, 1980, Elberse *et al.*, 1983). Biomass production increases with increasing nutrient content. So, the soil fertility is important for the species richness and species composition of grasslands (Grime, 1979; Huston, 1979; Tilman, 1988). On fertile soils, species with a high level of nutrient resorption dominate (Janiesch, 1973; Huston, 1979; Dierschke & Vogel, 1981). These very competitive species are generally characterized by (Grime, 1984; Grime & Huston, 1975): 1) a tall growing habitus, 2) a growth form which enables the environment to be intensively exploited, 3) a high potential growth rate and 4) the ability to make a thick layer of litter (Grime, 1973). Under favourable circumstances tall growing species with a high maximum growth rate are very competitive while species characteristic of less fertile soils are ousted (Aperdannier, 1959; Yemm & Willis, 1962; Harper, 1970). The latter species lack light and space and their germination is also adversely affected (Grime & Jeffrey, 1965). The nutrient content of the soil is strongly affected by manuring. In this manner manuring strongly influences the production of grasslands and consequently also their species richness and species composition. After manuring growth rate increases but hardly any reserves of nutrients are stored in the plant parts.

In contrast, in a poor, unmanured grassland the tall growing species quickly consume their small food supply. In these unfavourable circumstances they stop growing and are susceptible to diseases. In the unmanured very species-rich permanent plots in Rothamsted (Thurston, 1969) no species reached dominance, the vegetation was short and the biomass production was low. Species characteristic of relatively infertile soils like *Scabiosa columbaria* start growing slowly, have a relatively low growth rate and need only a small nutrient pool. After manuring they show hardly any increase in growth rate but they use the extra nutrients to build up reserves of food (Stuart Chapin, 1980). This enables them to grow longer when the nutrient pool diminishes and to survive periods of extremely low nutrient availability; for instance, drought (Bradshaw *et al.*, 1964; Rorison, 1967; Grime, 1979; Stuart-Chapin, 1983).

In 1994 the biomass of the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I), characteristic of the spared zone, was significantly larger (7.3 ton dw.ha^{-1}) than of communities III and IV. The relatively large peak standing crop of community I was probably caused by the fact that it had been badly managed for two or three years just before the reconstruction which raised the biomass production. In the future it can be expected that the species richness of this community will further decrease and that the rarer species in this plant community will disappear unless management practices are applied which decrease the biomass production. The relatively small peak standing crop (4.2 ton dw.ha^{-1}) of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV) in 1994 was probably caused by an incomplete development of the vegetation; the root system of the plants had not yet developed optimally and this retarded the above-ground production. Vegetations like this can be found on compacted soils which contain insufficient oxygen to enable roots to develop optimally. When soil organisms loosen such soils, roots develop, biomass production increases and the vegetation composition changes. It was for this reason that community IV dwindled every year and had almost disappeared in 1994.

In 1994 the annual productions of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) (7.6 ton.ha^{-1}) and the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) (8.0 ton dw.ha^{-1}) were significantly smaller than of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) (11.3 ton dw.ha^{-1}) and the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) (11.0 ton dw.ha^{-1}). The annual production of the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) (8.7 ton dw.ha^{-1}) was intermediate.

4.5 CONCLUSIONS

After the reconstruction of river dikes the seedbank has mostly disappeared. Because of this, immigration of plant species by seed dispersal and germination and seedling establishment are important regeneration characteristics. Species have to immigrate from the neighbourhood. Due to the fact that species-rich river dike vegetation is very scarce nowadays, the vegetation development on reconstructed dikes will take very long. Sparing a part of the vegetation provides a source of which species disperse to the reconstructed parts of the dike. Replacing the former top layer which contains propagules of the former vegetation, accelerates the vegetation development.

In the first few years after the reconstruction there was a large variation in the proportion of the annual and biennial pionieer species. In all methods of reconstruction these pioneer species decreased rapidly and almost disappeared. In the first four years after the reconstruction differences in vegetation composition and diversity were mainly caused by the different methods of reconstruction. After 1990 the vegetation closed and the biomass increased. As the management influences the biomass production and also the canopy structure, the impact of the management on the vegetation composition and diversity increased after 1990.

Methods of reconstruction

In 1990, four years after the reconstruction, differences in vegetation composition were still related to the differences in method of reconstruction. In 1994, eight years after the reconstruction, the best developed commmunity *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) still only occurred in the section with the spared zone. In 1994 this commmunity appeared mostly in the spared zone, but also in some permanent plots on replaced topsoil and on imported clay, directly bordering the spared zone. This implies that species dispersed from the spared zone to the replaced topsoil and the imported clay. The proximity of the spared zone appeared to be crucial.

Vegetation development was most spectacular on the replaced topsoil. In particular the development to the relatively species-rich *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) shows the importance of the replacement of the topsoil. The vegetation development on replaced subsoil and on imported clay was relatively slow.

In 1987 the sequence of the methods of reconstruction in terms of decreasing number of species was: complete sods - spared zone - replaced topsoil - replaced subsoil - imported clay. In 1994 this sequence was: spared zone - replaced subsoil - replaced topsoil - imported clay - complete sods. So, in 1987 species richness was highest on the complete sods, whereas in 1994 it was lowest of all methods of reconstruction, mainly due by management. This emphasizes the importance of the management after the reconstruction.

Sowing

Sowing seeds gathered locally (LGM) on topsoil appeared to accelerate the development of the vegetation. Addition of *Lolium multiflorum* did not seem to affect the development. The development of the unsown permanent plots was somewhat slower but by 1994 they had reached the same stage. Sowing with BG5 containing much *Lolium perenne* seemed to retard the vegetation development.

Management

Vegetation change can be manipulated by management, even under the unfavourable situation of long and narrow embankments (unfavourable area/perimeter ratio) bordering intensively used agricultural land. The time and frequency of cutting may be related to the growth of important species in the sward, whether to control dominant and aggressive grass species at the peak of growth or to allow rare plant species to complete their life cycle. Plant species must be able to produce seed occasionally. If management is inappropriate, the relatively expensive method of reconstruction replacing complete sods will be wasted labour because most of the species will still disappear.

With respect to the proportions in terms of percentages of either of the plant communities distinguished, a general trend in the sequence of the management regimes can be seen. Hay-making twice a year is considered to be good management, hay-making in June in combination with mulching in September, hay-making once a year in September, hay-making once a year in June and hay-making in June in combination with grazing in September as moderate management, whereas mulching twice a year, hay-making once every two years in September, grazing throughout the summer season, grazing twice a year, grazing in June in combination with hay-making in September, burning of the vegetation and no management are considered to be bad management practices.

In 1994 the sequence of the management practices with respect to an increasing number of species this sequence was: 1) hay-making twice a year, 2) hay-making in June in combination with grazing in September, 3) hay-making once a year in September, 4) hay-making in June in combination with mulching in September, 5) hay-making once a year in June, 6) hay-making once every two years in September, 7) mulching twice a year, 8) grazing twice a year, 9) no management, 10) grazing in June in combination with hay-making in September, 11) grazing throughout the summer season and 12) burning of the vegetation.

Plant communities

In 1994 the peak standing crops of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) and the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) were significantly smaller than of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) and the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). The peak standing crop of the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) was significantly larger than of community III and the *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV).

Appendix 1. Distribution (%) of the relevés among the plant communities in the combinations of the method of reconstruction and the management practices in 1987 and 1994.

Method of reconstr.	Management	year	N	Plant community I	II	III	IV	V	VI	VII	VIII	IX
Spared zone	2xM+r	1987	2	100	.	.	.	.	.	.	.	.
	2xM+r	1994	2	100	.	.	.	.	.	.	.	.
	2xM-r	1987	1	100	.	.	.	.	.	.	.	.
	2xM-r	1994	1	100	.	.	.	.	.	.	.	.
	2xM+-r	1987	1	100	.	.	.	.	.	.	.	.
	2xM+-r	1994	1	100	.	.	.	.	.	.	.	.
	1xM+r-el	1987	1	100	.	.	.	.	.	.	.	.
	1xM+r-el	1994	1	100	.	.	.	.	.	.	.	.
	1xM+r-lt	1987	2	100	.	.	.	.	.	.	.	.
	1xM+r-lt	1994	2	100	.	.	.	.	.	.	.	.
	1xM/2y-lt	1987	1	100	.	.	.	.	.	.	.	.
	1xM/2y-lt	1994	1	100	.	.	.	.	.	.	.	.
Replaced sods	2xM+r	1987	1	.	.	100	.	.	.	.	.	.
	2xM+r	1994	1	.	.	100	.	.	.	.	.	.
	2xM-r	1987	1	.	.	100	.	.	.	.	.	.
	2xM-r	1994	1	.	100	.	.	.	.	.	.	.
	1xM+r-lt	1987	1	.	.	100	.	.	.	.	.	.
	1xM+r-lt	1994	1	.	100	.	.	.	.	.	.	.
	1xM/2y-lt	1987	1	.	.	100	.	.	.	.	.	.
	1xM/2y-lt	1994	1	.	100	.	.	.	.	.	.	.
Replaced topsoil	2xM+r	1987	15	.	.	7	7	20	20	33	.	13
	2xM+r	1994	15	.	.	47	.	53	.	.	.	.
	2xM+-r	1987	3	.	.	33	33	.	33	.	.	.
	2xM+-r	1994	3	.	.	67	.	33	.	.	.	.
	2xM-r	1987	12	.	.	8	8	17	25	42	.	.
	2xM-r	1994	12	.	25	33	.	33	8	.	.	.
	1xM+r-el	1987	7	.	.	14	14	14	29	29	.	.
	1xM+r-el	1994	7	.	29	29	.	29	14	.	.	.
	1xM+r-lt	1987	13	.	.	8	8	8	39	39	.	.
	1xM+r-lt	1994	13	.	23	23	.	54	.	.	.	.
	1xM/2y-lt	1987	9	.	.	11	11	.	33	44	.	.
	1xM/2y-lt	1994	9	.	56	11	.	33	.	.	.	.
	Gseas	1987	5	.	.	.	.	20	20	60	.	.
	Gseas	1994	5	.	.	20	.	40	40	.	.	.
	2xG	1987	8	.	.	.	13	13	13	63	.	.
	2xG	1994	8	.	.	13	13	25	50	.	.	.
	G+M	1987	3	.	.	.	.	.	67	33	.	.
	G+M	1994	3	.	.	.	.	67	33	.	.	.
	M+G	1987	6	.	.	.	17	17	17	50	.	.
	M+G	1994	6	.	.	33	.	33	33	.	.	.
	Burning	1987	2	.	.	50	50	.	.	.	.	.
	Burning	1994	2	.	100	.	.	.	.	.	.	.
	No manag	1987	2	.	.	.	.	.	50	50	.	.
	No manag	1994	2	.	100	.	.	.	.	.	.	.

Method of reconstr.	Manage-ment	year	N	Plant community I	II	III	IV	V	VI	VII	VIII	IX
Replaced subsoil	2xM+r	1987	8	.	.	.	.	.	50	25	.	25
	2xM+r	1994	8	.	.	.	.	75	25	.	.	.
	2xM-r	1987	5	.	.	.	.	.	60	40	.	.
	2xM-r	1994	5	.	.	.	.	60	40	.	.	.
	2xM+-r	1987	1	.	.	.	.	.	100	.	.	.
	2xM+-r	1994	1	.	.	.	.	100	.	.	.	.
	1xM+r-el	1987	3	.	.	.	.	.	67	33	.	.
	1xM+r-el	1994	3	.	.	.	.	67	33	.	.	.
	1xM+r-lt	1987	6	.	.	.	.	.	67	33	.	.
	1xM+r-lt	1994	6	.	.	.	.	83	17	.	.	.
	1xM/2y-lt	1987	4	.	.	.	.	.	25	75	.	.
	1xM/2y-lt	1994	4	.	.	.	.	75	25	.	.	.
	Gseas	1987	1	.	.	.	.	.	.	100	.	.
	Gseas	1994	1	.	.	.	.	.	100	.	.	.
	2xG	1987	2	.	.	.	.	.	50	50	.	.
	2xG	1994	2	.	.	.	.	.	100	.	.	.
	G+M	1987	1	.	.	.	.	.	100	.	.	.
	G+M	1994	1	.	.	.	.	.	100	.	.	.
	M+G	1987	2	.	.	.	.	.	50	50	.	.
	M+G	1994	2	.	.	.	.	.	100	.	.	.
Imported clay	2xM+r	1987	5	.	.	.	.	.	.	40	60	.
	2xM+r	1994	5	.	.	.	.	80	20	.	.	.
	2xM-r	1987	5	.	.	.	.	.	.	20	80	.
	2xM-r	1994	5	.	.	.	.	80	20	.	.	.
	1xM+r-el	1987	2	.	.	.	.	.	.	.	100	.
	1xM+r-el	1994	2	.	.	.	.	100	.	.	.	.
	1xM+r-lt	1987	5	.	.	.	.	.	.	20	80	.
	1xM+r-lt	1994	5	.	.	.	.	80	20	.	.	.
	1xM/2y-l	1987	5	.	.	.	.	.	.	20	80	.
	1xM/2y-l	1994	5	.	.	.	.	100	.	.	.	.
	Gseiz	1987	4	.	.	.	.	.	.	50	50	.
	Gseiz	1994	4	.	.	.	.	.	75	25	.	.
	2xG	1987	6	.	.	.	.	.	.	33	67	.
	2xG	1994	6	.	.	.	.	33	50	17	.	.
	G+M	1987	3	.	.	.	.	.	.	33	67	.
	G+M	1994	3	.	.	.	.	.	67	33	.	.
	M+G	1987	4	.	.	.	.	.	25	25	50	.
	M+G	1994	4	.	.	.	.	50	50	.	.	.
	No manag	1987	1	.	.	.	.	.	.	100	.	.
	No manag	1994	1	.	.	.	.	100	.	.	.	.

CHAPTER 5

SPECIES COMPOSITION IN 1994 IN RELATION TO SOIL, BIOMASS, NUTRIENT REMOVAL AND VEGETATION STRUCTURE

5.1 INTRODUCTION

The species-rich grassland typical of Dutch river dikes requires special soil conditions (Yodzis, 1978; Sýkora & Liebrand, 1987; Van der Zee, 1992). In a period of 30 years the agricultural land use and the atmospheric nutrient deposition have changed these conditions to such a degree that species-rich grasslands on river dikes have almost disappeared. In 1992 only about 7% of the area of river dikes was covered by more or less species-rich grasslands belonging to the phytosociological syntaxa *Arrhenatheretum elatioris* and *Lolio-Cynosuretum* (Van der Zee, 1992). Only 1% was covered by the typical species-rich dry-grassland *Medicagini-Avenetum*.

The main differentiation in the floristic composition on river dikes is correlated with soil fertility, lime content and the intensity of mowing or grazing and also with aspect and slope (Grime & Lloyd, 1973; Van Heerden, 1979; Smith, 1980; Sýkora & Liebrand, 1988). The *Medicagini-Avenetum* appears to be more frequent on south and south-west facing slopes and on relatively infertile soils with a clay content below 25%. It occurs under a variety of management practices but is hardly ever fertilized (Van der Zee, 1992). Various subassociations can be distinguished within the *Medicagini-Avenetum* (Sýkora & Liebrand, 1988). The subassociations *agrostietosum tenuis* (Neijenhuijs, 1968) and the *centaureetosum scabiosae* (Neijenhuijs, 1968; Westhoff & Den Held, 1969) occur only on soils with a mean clay content ranging between 3% and 14%. In the soil under the latter subassociation Van der Zee (1992) measured clay contents of 3% to 10%. In the other subassociations the clay content varies between 17% and 24%. In contrast to heavier soils, sand is highly permeable to water, well aerated, poor in intrinsic nutrients and the adsorption capacity for K and NO_3 is low, with the consequence that these nutrients are quickly washed out.

Since about the beginning of the 20th century, vegetation has increasingly been characterized in terms of its floristic composition (Fliervoet, 1984). This practice is based on the assumption that, since all species have their characteristic ecological amplitude, floristic data are the most informative, describing vegetation in detail in relation to its habitat characteristics (Braun-Blanquet, 1928). Floristic data have indeed proved to be useful for an ecological identification of grasslands (Kruijne *et al.*, 1967; Klapp, 1965; Dirven & Wind, 1982). Additionally, plant features that are not relevant for the position in a taxonomical system, such as for instance the canopy structure, life form and phenology, may contain much information about the plant-habitat relationship of a species, a population or an individual. Such plant features can be successfully used for an ecological description of vegetation types.

The characterization of a vegetation by its structural composition should be done by examining and integrating the most important canopy variables (Fliervoet, 1984). Plots with the same biomass production may, for example, differ in vegetation pattern and canopy structure (Fliervoet, 1984; Bakker, 1989). A relatively open tall-growing vegetation may have the same biomass as a shorter, very dense vegetation. The density of the vegetation restricts the chance of plant species germinating and establishing (Grime, 1973, 1979; Grime *et al.*, 1981). Therefore, the species richness may be greater in the tall, open vegetation type than in the short, dense vegetation. Furthermore, the canopy structure of the vegetation, which determines both light penetration to the soil surface and micro-climate, seems to be an important determinant of the onset of germination and the subsequent fate of seedlings (Oomes & Elberse, 1976; Verkaar *et al.*, 1983; Fenner, 1995; Goldberg, 1987).

The overall species-richness of a research field is related to the vegetation pattern. This pattern depends on the management practices applied (Bakker, 1989). Comparing intensively grazed meadows with extensively grazed meadows reveals macro-patterns. Within grazed meadows, different grazing intensities can lead to micro-patterns consisting of a mosaic of heavily utilized areas and lightly utilized patches. Relatively high species numbers can be found in such mosaics.

Since grazing always implies foraging, trampling and manuring, it seems important to study the effects of all these types of impacts on the vegetation (Bakker, 1989). Foraging without manuring takes place if the animals only briefly graze terrains which are difficult to reach, like steep river dike slopes. Manuring without foraging takes place if the animals defaecate in latrines. These latrines are areas of local influence, resulting in the emergence of trampling indicators and nitrophilous plant communities. Latrines of sheep grazing river dikes are only found on the level tops or feett of the dikes, or, when these are not available, on less steep parts of the dike slopes. These differences in intensity of foraging, trampling and manuring lead to micro-patterns in the vegetation.

Accepting species diversity to be a major objective in conservation management, a large standing crop and litter should be prevented (Grime, 1973, 1979) and a short turf should be aimed at, at least locally (Job & Taylor, 1978). Only part of the production should be consumed and this percentage should vary in space, since foraging at different intensities is considerd an advantage for the establishment of vegetation patterns of varying canopy structure, i.e. a mosaic of short turf and tall turf (Klapp, 1965; Oosterveld, 1975; Harper, 1977).

In the light of the theories mentioned above the relation between the species composition in 1994 and the soil composition, biomass, nutrient removal and the vegetation structure is studied on a reconstructed river dike.

5.2 METHODS

In order to restore former species-rich plant communities on an experimental river dike several methods of reconstruction were applied. The impact of the methods of reconstruction was investigated by describing the succession. Several species attributes and community characteristics were used to explain successional sequences, such as life-forms, rarity, species richness and phytosociological composition (see Chapter 3). The impact of method of reconstruction, sowing and management on vegetation development between 1987 and 1994 is dealt with in chapter 4.

In this chapter the structural composition of the vegetation is characterized by examining and integrating the following canopy variables: 1) above-ground biomass and annual crop production, 2) nutrient removal by management, 3) vegetation pattern, 4) canopy structure and 5) light penetration.

5.2.1 Soil research

It is obvious that the vegetation development between 1987 and 1994 and the composition of the vegetation in 1994 will have been influenced by the soil composition of the experimental river dike (see Chapter 3 and Sýkora & Liebrand, 1987; Van der Zee, 1992). The physical and chemical attributes of the soil on the experimental dike were determined and were then used to calculate the mean values of the various attributes of the plant communities distinguished. Means were also calculated for the methods of reconstruction so that these methods could be compared. In addition, the variation within the methods of reconstruction was determined, to ascertain whether the soil used in these methods was homogeneous.

Sampling and analysis

On 8 October 1990 the soil in 28 permanent quadrats dispersed over the experimental dike was sampled with a soil auger with a diameter of 2 cm. Eight sub-samples were taken per permanent quadrat at depths of 0.5 to 10.5 cm below the ground. The sub-samples of each permanent quadrat were mixed. The samples were dried at 25°C, crushed gently, and then sieved to the <2 mm fraction (i.e. clay). They were stored in paper bags until the analysis was performed. Before the analysis the samples were dried again for 24 hours at 25°C. For an exact description of the soil analysis see the manual of the laboratory of the Department of Soil Science and Plant Nutrition of Wageningen Agricultural University, where the soil analysis was performed (Houba *et al.*, 1985, 1986, 1987).

Granular composition
The following fractions were determined:
- clay: <2 μm,
- silt: 2 μm - 50 μm,
- sand: 50 μm - 2 mm.

The method of analysis of the granular composition is based on the difference in sedimentation rate between heavier and lighter soil parts. The organic material present was decomposed with the help of hydrogen peroxide. For further explanation see the above-mentioned manual. The clay and sand contents were measured directly. The content of the silt fraction was calculated on the basis of measured clay and sand fractions.

Chemical attributes of the soil
The following chemical attributes were determined:
- acidity: pH-H_2O,
- lime content: $CaCO_3$ %,
- electrical conductivity (EC),
- organic matter content: humus %, and C/N quotient,
- nitrogen content: N_{total} % and N_{total} (mg/kg),
- phosphorus content: P_{total} % and P_{total} (mg/kg),
- potassium content: K (mg/kg),
- sodium content: Na (mg/kg),
- calcium content: Ca (mg/kg).

A 0.01 M $CaCl_2$ solution was used to extract soluble chemical fractions. Only these fractions are immediately available to the plants. The methods described by Houba *et al.* (1986, 1987) were followed to determine the soluble fractions in the extracts.

Acidity (pH-H_2O) and lime content ($CaCO_3$ %)
The acidity was potentiometrically measured in distilled water (pH-H_2O) which was in equilibrium with a soil suspension after the soil particles had settled. The measurement was performed by means of a glass electrode and a calomel electrode. The lime content was defined according the Scheibler method.

Electrical conductivity (EC)
The electrical conductivity was defined potentiometrically in distilled water which was in equilibrium with a soil suspension after the soil particles had settled. The measurement was performed by means of a glass electrode and a calomel electrode.

Nitrogen (N_{tot} %, NO_3-N, NH_4-N, N-mineral)
The total nitrogen content was initially defined after destruction with an aggressive solution (salicylic acid in a H_2SO_4-Se mixture) which liberates both the nitrogen that is easily available to plants and the nitrogen which is not available, or is poorly available. The measured nitrogen content is the total nitrogen percentage (N_{tot} %). Soil contains various soluble nitrogen-containing compounds, consisting of nitrate (NO3-N), ammonia (NH4-N) and - the remainder - soluble organic nitrogen (org-N). The amounts of nitrogen supplied by NO_3 and NH_4 were defined in a 0.01 M $CaCl_2$ solution. The amount of N-mineral was defined by totalling the values for N-NO_3 and N-NH_4.

Organic material and C/N quotient

The organic matter content was determined according to the Kurmies method. The C/N quotient was defined by taking 58% of the organic matter as carbon content and dividing this value by the total nitrogen content (N_{tot} %). The C/N quotient of the soil of the experimental dike was defined on the basis of analysing the samples from 28 locations in 1990.

Phosphorus (P_{tot} %, P_2O_5, P)

The total phosphorus content (P_{tot} %) was first defined after destruction with an aggressive solution (salicylic acid in a H_2SO_4-Se mixture). The content of P_2O_5/100 g was calculated from P_{tot} % by using the formula:

P_{tot} % x 71.000/31 = P_2O_5/100 g (M_{P2O5} = 71, M_P = 31).

The amount of phosphorus easily available to plants was defined in a 0.01 M $CaCl_2$ extract.

Potassium, sodium, and magnesium

Potassium, sodium and magnesium contents were determined in a 0.01 M $CaCl_2$ solution. An emission spectrophotometry method was used for the analysis of the K and Na contents. Mg was measured using an absorption spectrophotometry method.

N/P in vegetation

The N/P quotient in plant tissue was defined on the basis of the results of analysing samples from 30 locations in 1994. Vegetation samples were taken at all 30 locations; at 18 of these locations, root samples were taken as well.

Nitrogen mineralization

In 1994 the nitrogen mineralization was determined in 78 permanent quadrats. Nitrogen mineralization in grasslands on nutrient-rich soils is suggested to be especially apparent between March and June (Olff, 1992; Schaffers, 1995). Berendse *et al.* (1994) found that in dry meadows nitrogen mineralization peaked in spring but in wet meadows it peaked in summer. Therefore, in this study nitrogen mineralization was determined only in spring and early summer. Measurements were performed in two successive periods of 6 weeks: period I; 28 March - 9 May and period II; 9 May - 20 June. On each sampling date five pairs of soil samples were taken per permanent quadrat. The samples were taken with a 4 cm diameter polyvinyl chloride tube so that the sample was a relatively undisturbed column of the first 10 cm of the soil. One of each pair of samples was transported to the laboratory in a cooled box and mineral N was extracted within 24 h after being collected. In some cases the sub-samples were dried and stored in paper bags until the analysis was performed. The other tube was put back in the soil after the top had been closed with a plastic lid, in order to measure the accumulation of mineral N during the subsequent incubation period. The lid prevented rain water moving through the tube, but air was allowed to enter through four holes that remained above the soil surface during incubation.

The increase in the inorganic nitrogen content N-mineral (NO_3 + NH_4) in the incubation periods is a measure of nitrogen mineralization. The increase was determined as the difference of the inorganic nitrogen content between incubated sub-samples and sub-samples taken at the beginning of the incubation period. The amounts of nitrogen supplied by NO_3 and NH_4 were defined in a 0.01 M $CaCl_2$ solution. The amount of N-mineral was defined by totalling the values for N-NO_3 and N-NH_4. The nitrogen mineralization expressed in mg kg^{-1} in 12 weeks was converted into nitrogen mineralization in kg ha^{-1} in 12 weeks and in g day^{-1} ha^{-1} by means of the specific gravity of the soil.

5.2.2 Above-ground biomass and annual crop production

At 93 locations (92 on the experimental dike and 1 in a dry floodplain grassland vegetation) the above-ground biomass of the vegetation (kg dry matter ha^{-1}) was measured one or more times a year in 1988, 1989, 1990, 1992 and 1994, just before mowing or grazing. The biomass in unmown plots was determined at the same time, to allow a comparison. Exclusion cages were used for measuring the biomass production in the meadows. These cages were moved each year.

The above-ground biomass in spring of all locations was compared. Additionally, the total production per year of locations managed twice a year was obtained by totalling both measured values. The above-ground biomass was measured by clipping the vegetation just above the ground surface in 4 randomly chosen sub-plots of (25 x 25) cm^2 in each of the permanent quadrats, including standing dead material, and excluding litter and bryophytes. Dry weights were measured after drying at 70°C for 48 h.

In many studies, biomass is defined as 'peak standing crop' (maximum above-ground biomass) in July. In the present study the biomass was measured in June and September, so the peak standing crop was not actually measured. According to Oomes (1992) the peak standing crop is 62% (± 5%) of the year production. In this research the year production was determined at 137 locations (40 in 1988, 46 in 1989 and 51 in 1990). When calculating the proportion of the spring production in the annual production, the spring production measured was compared with the peak standing crop. To trace if there was any change in this percentage (spring production/year production * 100%) between 1988 and 1990, this percentage was determined in 37 locations managed twice yearly in 1988, 1989 and 1990. Of these locations, 29 were mown twice a year and 8 were grazed twice a year or mown and grazed once a year. The mean biomass in June (i.e. peak standing crop) and the annual biomass production were calculated per plant community, per method of reconstruction, per seed mixture applied and per management practice.

5.2.3 Nutrient removal by management

In the Netherlands, the mean atmospheric deposition of inorganinic nitrogen is estimated to be between 40 and 50 kg N $ha^{-1}.yr^{-1}$ (Fransen, 1987; Schneider & Bresser, 1988; Bobbink *et al.*, 1990; Van Dam, 1990). The deposition of P is estimated to be between 0.3 and 1.7 kg $ha^{-1}.yr^{-1}$ with a mean value of 1 kg ha^{-1}. yr^{-1} and the deposition of K is estimated to be between 10 and 20 kg $ha^{-1}.yr^{-1}$ with a mean value of 15 kg $ha^{-1}.yr^{-1}$ (Katznelson, 1977; Marrs *et al.*, 1983; Heij & Schneider, 1991). To gain a net removal of nutrients the amount of nutrients removed with the mowings should exceed the amounts of atmospheric deposition.

On 21 June 1994, the biomass in 30 permanent quadrats dispersed over the experimental dike was sampled. The above-ground vegetation was clipped to 0.5 cm height in 4 replicate sub-samples of 0.25x0.25 cm per permanent quadrat. The sub-samples of each permanent quadrat were mixed. At 18 of the locations, root samples were taken as well. The samples were dried 48 hours at 70°C and stored in paper bags until analysis. Before the analysis the samples were dried again for 24 hours at 25°C. N and P contents in the plant material were determined as in the soil samples (see § 5.2.1). K contents were determined by atomic absorption spectrometry. For an exact description of the biomass analysis see the manual of the laboratory of the Department of Soil Science and Plant Nutrition of Wageningen Agricultural University, where the biomass analysis was performed (Houba *et al.*, 1985; 1986; 1987).

The following chemical attributes were determined: 1) nitrogen content: N_{total} % and N_{total} (mg/kg), 2) phosphorus content: P_{total} % and P_{total} (mg/kg) and 3) potassium content: K (mg/kg). For methods of analysis, see § 5.2.1. The N/P quotient was defined on the basis of the results of analysing samples from 30 locations in 1994. Vegetation samples were taken at all 30 locations; at 18 of these locations, root samples were taken as well.

5.2.4 Vegetation pattern

Species richness was analysed in four plots of 0.25 m^2, in four plots of 1.00 m^2 and in the entire permanent quadrat of 24 m^2. First, the numbers of species in the four smallest plots in the corners of the permanent quadrats were analysed (see figure 24). Subsequently these four plots were expanded to 1 m^2 and all new species were noted. Finally, the entire permanent quadrat (24 m^2) was analysed according the Braun-Blanquet method. Graphs were drawn, in which species richness was plotted against the surface area. Vegetation patterns were only visualy observed without actively measuring and mapping the boundaries of the heavily and lightly grazed areas.

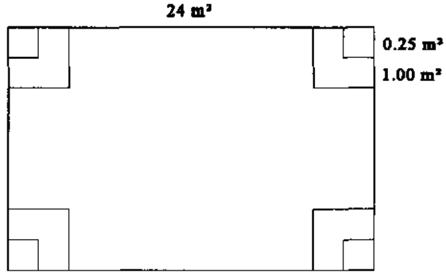


Figure 24. Schematic survey of permanent quadrats of 24 m^2 with trail plots of 0.25 m^2 and 1 m^2.

5.2.5 Canopy structure

In this thesis canopy structure is defined as the composition of the vegetation in terms of its morphological elements, taking account of both the horizontal and vertical arrangement of these elements (i.e. the architecture of the stand). In this part of the study the above-ground biomass determined per vegetation layer was used to characterize the vertical stand structure of the grassland types under different management practices.

The stratified yield of the above-ground biomass was used to analyse canopy structure. These structure analyses were made during the main flowering period of the grassland types. During the main flowering period the grassland vegetation has reached its maximum height, there is a maximum accumulation of above-ground biomass, and the fully developed canopy structure is characterized by the greatest number of flowering plants. In the grassland types concerned here, this period is usually from mid-June to the end of June. On 16 locations one of the four sub-samples for the above-ground biomass definition (see § 4.2.2) was harvested at 10 cm intervals from the ground to the top of the vegetation. Dry weights of the sub-samples were measured separately after drying at 70°C for 48 h. In addition to the total above-ground biomass, the proportional distribution of the biomass over the height was calculated with the help of the data from the separate heights.

5.2.6 Light penetration

The ratio of light flux below the vegetation to light flux above it is called the proportional penetration of light through the vegetation (Tilman, 1993). In 1994 proportional light penetration was measured in 75 permanent quadrats at the time of mowing in June. A photometer consisting of a registration unit with two photosensitive cells was used to measure the difference in light intensity above and below the vegetation. One photosensitive cell was placed under the vegetation to measure the amount of blue, green, red and far red light and the total intensity of light under the vegetation (in µmol/m^2/s). The second photosensitive cell was placed above the vegetation during the measurement and measures only the total intensity of light (in W/m^2). This reference value was used to calculate the proportional penetration of light. The light was measured at four sites in each permanent quadrat. The chosen sites represented the differences in the vegetation structure in the permanent quadrat. All light measurements were performed during the same day, to minimize differences in weather conditions and intensity of light.

5.2.7 Species composition in 1994

Impact of method of reconstruction

The five methods of reconstruction were analysed in terms of: 1) mean species richness, 2) mean number of grassland species, 3) proportion (%) of syntaxonomical elements (weighted by cover abundances of the plant species), 4) proportion (%, weighted) of the main ecological species groups (based on phytosociological syntaxa): grassland species, plants of trampled areas, ruderal species, pioneer species and remaining species and 5) proportions (%, weighted) of the national rarity categories in 1980. A synoptic table showing the five methods of reconstruction was constructed. In this table the exclusively differential species and the species differential for several methods of reconstruction were boxed.

Impact of sowing

The seven sowings applied were analysed by the mean species richness and the mean number of grassland species. The grassland species were distinguished by classifying them into ecological groups (Arnolds & van der Maarel, 1979; Arnolds & van der Meijden, 1976; van der Meijden *et al.*, 1984). For this the following ecological groups were selected: damp fertilized grasslands, dry neutral grasslands, chalk grasslands and dry acid grasslands. On part of the experimental dike where only the subsoil had been replaced, four different mixtures were sown. These sowing mixtures were examined separately by analysing the mean species richness and the mean number of grassland species.

Impact of management

The twelve management practices were analysed in terms of: 1) mean species richness, 2) mean number of grassland species, 3) proportion in terms of percentage of phytosociological syntaxa (weighted by cover abundances of the plant species), 4) proportion (%, weighted) of the main phytosociological syntaxa: grassland species, plants of trampled areas, ruderal species, pioneer species and remaining species and 5) proportions (%, weighted) of the national rarity categories in 1980.

Impact of management on plant species

The impact of the management was determined for all species in 1994. The two main grass species on the experimental river dike are *Arrhenaterum elatioris* and *Lolium perenne*. *Arrhenaterum elatioris* is a typical species of hay-making areas whereas *Lolium perenne* is typical of grazed areas.

Additionally, the impact of the management was determined for two other grass species (*Elymus repens* and *Trisetum flavescens*), twelve target species (*Centaurea jacea, Crepis biennis, Crepis capillaris, Daucus carota, Galium mollugo, Heracleum sphondylium, Lathyrus pratensis, Leucanthemum vulgare, Ranunculus bulbosus, Tragopogon pratensis ssp. orientalis, Veronica chamaedrys* and *Vicia cracca*), eight common grassland species (*Bellis perennis, Medicago lupulina, Ranunculus repens, Symphytum officinalis, Trifolium dubium, Trifolium repens, Vicia sativa ssp. nigra* and *Vicia sepium*) and four unwanted species (*Cirsium arvense, Cirsium vulgare, Rubus caesius, Urtica dioica*).

5.2.8 Statistics

ANOVA was used to explore separately the relationship between the dependent variables considered in this chapter and the independent variables plant community, method of reconstruction, sowing and management (see also § 2.4). The data set of the light penetrations appeared to be skewed for all light parameters. Therefore, it was log10 transformed prior to the analysis. All other data sets were normally distributed. Differences are tested with a oneway ANOVA followed by a Least Significance Difference (LSD) test. Treatments which are significally different are assigned to different homogeneous groups. Homogeneous groups with one or more characters in common are not significantly different. Pearson product-moment correlation with two-tailed probabilities was used to determine the relation between the soil parameters and between the number of species and the biomass.

5.3 RESULTS

5.3.1 Soil characteristics

Soil characteristics of the experimental dike

Table 40 shows a large variation in the measured physical and chemical attributes of the soil of the experimental dike. Because of this heterogeneity it is to be expected that there will be variation in the ultimate vegetation. The ultimate vegetation on the whole experimental dike will not be homogeneous.

Table 40. Mean, maximum and minimum values of the physical and chemical attributes of the soil of the experimental dike.

Soil attributes	Mean	Max.	Min.
Clay %	27.0	38.1	16.2
Silt %	34.8	42.5	22.6
Sand %	38.2	60.6	22.7
pH-H_2O	7.8	7.9	7.6
$CaCO_3$ %	4.56	9.01	0.97
Electr. cond. (EC)	230	306	164
Organic matter %	1.58	2.62	1.16
N_{total} $mg.kg^{-1}$	1530	2940	553
N_{total} %	0.15	0.29	0.06
P_{total} $mg.kg^{-1}$	482	698	271
P_{total} %	0.05	0.07	0.03
Na $mg.kg^{-1}$	504	626	362
K $mg.kg^{-1}$	8611	10581	5856
Ca $mg.kg^{-1}$	14983	22923	5375

Correlations between physical and chemical attributes

The clay content correlated positively ($p<0.01$) with the electrical conductivity, the organic matter content, the total nitrogen content, the potassium content and the C/N quotient, and negatively ($p<0.01$) with the sand content, the acidity, the lime content and the calcium content (see table 41).

Table 41. Pearson correlation coefficients between the physical and chemical attributes of the soil of the experimental river dike.

Attrib.	Clay	Silt	Sand	pH	EC	CaCO3	Org.mat	Ntot	Ptot	K	Ca	CN
Silt-%	.60**											
Sand-%	-.92**	-.87**										
pH	-.77**	-.45*	.70**									
EC	.88**	.61**	-.85**	-.71**								
CaCO3	-.63**	-.32	.55*	.77**	-.46*							
Org. mat	.53*	.32	-.49*	-.65**	.60**	-.40						
Ntot	.46*	.30	-.44*	-.74**	.44*	-.53*	.70**					
Ptot	.29	.21	-.29	-.63**	.21	-.57**	.42	.74**				
K	.89**	.71**	-.90**	-.67**	.77**	-.65**	.52*	.53*	.42			
Ca	-.54*	-.22	.44*	.68**	-.40	.90**	-.21	-.40	-.44*	-.54*		
CN	-.42	-.43	.47*	.36	-.36	.45*	-.11	-.54**	-.47**	-.58*	.36	
NP	.51*	.35	-.49*	-.63**	.54*	-.41	.74**	.88**	.36	.53*	-.29	-.40

N of cases: 28; 1-tailed significance: * = p < -0.01, ** = p < -0.001

Soil characteristics of the plant communities

Tables 42 and 43 show the most important physical and chemical soil attributes of the seven plant communities in 1994. The mean clay proportion varied between 22.2% (heavy loam) and 30.2% (light clay). The proportion of clay was significantly ($p<0.05$) lowest in the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) and highest in the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) (see table 41). Community I was the only community occurring on heavy loam (i.e. clay% 17.5 - 25%). All other communities were found on light clay (i.e. clay% 25 - 35%). The proportion of sand varied between 31.7% and 44.4% and was lowest in community III and in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II).

The pH and the CaCO3 content were highest in community I (see table 41). The differences in pH are very small. All communities occurred on slightly basic soils (Schachtschabel *et al.*, 1976). Other soil characteristics of the plant communities are presented in appendix 1 (see page 153).

Table 42. Mean content of clay and sand per plant community. Homogeneous groups at $p<0.05$ level.

Plant comm.	Clay %	Homogeneous groups	Plant comm.	Sand %	Homogeneous groups
I	22.2	a . .	III	31.7	a .
V	25.7	. b .	II	33.4	a .
VI	25.9	. b .	IV	34.5	a b
II	28.0	. b c	V	41.3	. b
VII	28.3	. b c	VI	42.3	. b
IV	29.9	. b c	I	43.4	. b
III	30.2	. . c	VII	44.4	. b

Table 43. Mean pH and CaCO3 content per plant community. Homogeneous groups at $p<0.05$ level.

Plant comm.	pH	Homogeneous groups	Plant comm.	CaCO3 %	Homogeneous groups
I	7.81	a .	I	6.84	a . .
IV	7.81	a b	IV	5.61	a b .
VI	7.78	a b	II	4.75	. b .
V	7.76	. b	III	4.70	. b .
VII	7.76	. b	V	4.61	. b .
II	7.76	. b	VI	4.08	. b c
III	7.75	. b	VII	2.34	. . c

Soil characteristics of the methods of reconstruction

The imported clay and the spared zone had a significantly ($p<0.05$) lower clay content and a significantly higher sand content than most other methods of reconstruction (see table 44). Of all methods of reconstruction the clay content of the replaced complete sods was significantly highest and the sand content lowest.

Table 44. Mean content of clay, silt and sand per method of reconstruction. Homogeneous groups at $p<0.05$ level.

Method of reconstr.	Clay %	Homogeneous groups	Method of reconstr.	Silt %	Homogeneous groups	Method of reconstr.	Sand %	Homogeneous groups
Imp. clay	22.4	a . .	Sp. zone	31.9	a .	Imp. clay	45.4	a . . .
Sp. zone	23.1	a . .	Subsoil	32.1	a .	Sp. zone	45.0	a . . .
Subsoil	27.0	. b .	Imp. clay	32.2	a .	Subsoil	40.9	. b . .
Topsoil	28.7	. b .	Topsoil	36.4	. b	Topsoil	34.9	. . c .
Sods	38.1	. . c	Sods	39.2	. b	Sods	22.7	. . . d

The pH and the CaCO3 content of the spared zone and the imported clay were significantly ($p<0.05$) higher compared with the other methods of reconstruction (see table 45). The differences in pH were very small and are probably ecologically insignificant.The electrical conductivity was significantly higher in the sods and the topsoil than in the other methods of reconstruction but the differences were only slight. The organic matter content was low in all cases, being highest in the replaced complete sods and lowest in the subsoil.

Table 45. Mean pH, CaCO3-%, EC and organic matter-% per method of reconstruction. Homogeneous groups at p<0.05.

Method of reconstr.	pH	Homogeneous groups	Method of reconstr.	CaCO3 %	Homogeneous groups
Imp. clay	7.84	a . . .	Sp. zone	7.99	a . . .
Sp. zone	7.80	. b . .	Imp. clay	5.86	. b . .
Subsoil	7.74	. . c .	Topsoil	4.07	. . c .
Topsoil	7.73	. . c .	Subsoil	3.39	. . . d
Sods	7.66	. . . d	Sods	2.81	. . . d

Method of reconstr.	EC	Homogeneous groups	Method of reconstr.	Organic mat-%	Homogeneous groups
Imp. clay	202	a . .	Sods	2.62	a . . . .
Subsoil	212	a . .	Sp. zone	2.02	. b . . .
Sp. zone	220	a . .	Topsoil	1.67	. . c . .
Topsoil	242	. b .	Imp. clay	1.45	. . . d .
Sods	293	. . c	Subsoil	1.30	. . . . e

The total nitrogen and phosphorus contents were lowest in the imported clay (see table 46). The potassium content was significantly higher in the sods and the topsoil than in the other methods of reconstruction. The calcium content was highest in the spared zone and lowest in the subsoil.

Table 46. Mean N, P, K and Ca per method of reconstruction. Homogeneous groups at p<0.05 level.

Method of reconstr.	Ntot mg/kg	Homogeneous groups	Method of reconstr.	Ptot mg/kg	Homogeneous groups
Subsoil	1239	a . .	Imp. clay	425	a .
Imp. clay	1307	a . .	Sp. zone	478	. b
Topsoil	1648	. b .	Topsoil	510	. b
Sp. zone	1731	. b .	Subsoil	532	. b
Sods	2256	. . c	Sods	539	. b

Method of reconstr.	K mg/kg	Homogeneous groups	Method of reconstr.	Ca mg/kg	Homogeneous groups
Sp. zone	7521	a .	Sp. zone	22923	a . . .
Imp. clay	7983	a .	Imp. clay	17147	. b . .
Subsoil	8232	a .	Sods	14662	. b c .
Topsoil	9226	. b	Topsoil	13892	. . c .
Sods	10276	. b	Subsoil	12148	. . . d

The C/N ratio varied from 8.4 in the subsoil to 12.0 in the imported clay (table 47). The N/P ratio was highest in the complete sods and lowest in the imported clay. The complete sods differed most from the other methods of reconstruction. The clay content and silt content were high whereas the sand content was low. The sods had the lowest pH and the lowest CaCO3 content whereas the electrical conductivity and the contents of organic matter, total nitrogen, total phosphorus and potassium were the highest.

Table 47. Mean C/N and N/P ratio per method of reconstruction. Homogeneous groups at p<0.05 level.

Method of reconstr.	C/N	Homogeneous groups	Method of reconstr.	N/P	Homogeneous groups
Topsoil	10.3	a .	Subsoil	2.5	a . . .
Subsoil	10.5	a .	Imp. clay	3.0	. b . .
Sods	11.6	a b	Topsoil	3.3	. . c .
Sp. zone	11.7	a b	Sp. zone	3.6	. . c d
Imp. clay	12.0	. b	Sods	4.2	. . . d

5.3.2 Nitrogen mineralization

Plant communities

N-mineralization between 28 March and 20 June was highest in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) and significantly ($p<0.05$) lower in the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) and in the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) (see table 48).

Table 48. Mean N-mineralization between 28 March and 20 June per plant community in 1994. Homogeneous groups at p<0.05 level.

Plant community	Min_{tot} kg ha^{-1}	Homogen. groups
VI	19.7	a .
V	25.6	a .
III	29.3	a b
I	29.5	a b
II	37.5	. b

Table 49. Mean N-mineralization between 28 March and 20 June per method of reconstruction in 1994. Homogeneous groups at p<0.05 level.

Method of reconstr.	Min_{tot} kg ha^{-1}	Homogen. groups
Sp. zone	26.46	a .
Imp. clay	26.96	a .
Subsoil	28.22	a .
Topsoil	32.48	a .
Sods	49.29	. b

Methods of reconstruction

N-mineralization was highest in the replaced complete sods and lowest in the spared zone and in imported clay (table 49).

Management

In all management practices N-mineralization between 28 March and 9 May was higher than between 9 May and 20 June. In period I the mean N-mineralization over all management practices was 412 g day^{-1} ha^{-1} and in period II 265 g day^{-1} ha^{-1}.

N-mineralization was considerably higher in the burning regime than in all other management practices (see table 50). It was double the amount of the next highest case i.e. mowing twice a year without removal of the mowings. With mowing and removal once every two years and with grazing throughout the summer more than 30 kg $N_{mineral}$ was mineralized per ha. Mineralization was lowest under mowing in June in combination with grazing in September. The low N-mineralization under no management is striking.

Table 50. Mean N-mineralization between 28 March and 20 June per management practice in 1994. Homogeneous groups at p<0.05 level.

Management	N_{miner} kg ha^{-1}	Homogeneous groups
Burning	79.02	a . . . .
2xM-r	38.93	. b . . .
1xM+r/2y	37.10	. b c . .
Gseas	32.93	. b c d .
1xM+r-el	28.69	. b c d e
1xM+r-lt	26.46	. b c d e
2xM+r	25.39	. . c d e
G+M	23.60	. . c d e
2xM+-r	20.59	. . c d e
2xG	18.54	. . . d e
No manag	16.38	. . . d e
M+G	15.75	. . . . e

5.3.3 Peak standing crop and annual crop production in 1994

Plant communities

In 1994 the peak standing crop in the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) was significantly smaller than in the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I), in the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) and in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) (see table 51). The peak standing crop in the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) was intermediate.

Table 51. Mean peak standing crop and annual crop production per plant community in 1994. Homogeneous groups at p<0.05 level.

Plant comm.	Peak standing crop (ton ha^{-1})	Homogen. groups	Plant comm.	Annual production (ton ha^{-1})	Homogen. groups
III	5.9	a . .	III	7.6	a .
VI	6.2	a b .	VI	8.0	a .
I	7.3	. b c	I	8.7	a b
V	7.5	. . c	V	11.0	. b
II	8.3	. . c	II	11.3	. b

In all communities the annual crop production in 1994 was still relatively large and varied between 7.6 and 11.3 tons per ha. In 1994 the annual crop productions of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) and the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) were significantly smaller than of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) and the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). The annual production of the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) was intermediate.

Methods of reconstruction

In 1994 the largest biomass in June was measured on the replaced complete sods and the smallest biomass on the replaced topsoil (see table 52). The differences between the methods of reconstruction were not significant ($p<0.05$), due to the small number of observations.

Table 52. Mean peak standing crop per method of reconstruction under management 2xM+r in 1994.

Method of reconstr.	Biomass ton/ha
Topsoil	5.7
Spared zone	6.6
Imp. clay	7.1
Subsoil	7.2
Sods	8.4

Table 53. Mean peak standing crop per sowing under management 2xM+r in 1994.

Sowing	Biomass ton/ha
No sowing	7.8
D1	6.2
D1+LGM	6.0
BG5	6.8
BG5+LGM	6.1

Sowing

Only permanent plots with management hay-making twice a year were considered here. In 1994 the largest biomass in June was measured on permanent plots with no sowing and the smallest biomass on permanent plots with sowing BG5+LGM (table 53). The differences between the sowings were not significant ($p<0.05$), due to the small number of observations. Ecologically, the small differences are likely to be insignificant.

Management

Table 54 shows the peak standing crop per management and the homogeneous groups at the $p<0.05$ level in 1994. In 1994 a peak standing crop (i.e. biomass in June) smaller than 6 ton dry matter per hectare was only found under grazing extensively throughout the summer. A peak standing crop between 6 and 7 ton ha^{-1} was found under the three other grazing regimes and under hay-making twice a year. A peak standing crop larger than 8 ton ha^{-1} was found under mulching twice a year and under 'no management'.

Table 54. Mean biomass in June per management regime in 1994. Homogeneous groups at $p<0.05$ level.

Management	Biomass ton/ha	Homogeneous groups
Gseas	5.6	a . .
M+G	6.2	a b .
2xM+r	6.5	a b .
G+M	6.9	a b c
2xG	7.0	a b c
1xM+r-lt	7.0	a b c
2xM+-r	7.1	a b c
1xM+r-el	7.5	a b c
Burning	7.6	a b c
1xM+r/2y	7.8	. b c
2xM-r	8.1	. . c
No manag	9.0	. . c

Table 55 shows the standing crop per management and the homogeneous groups at the $p<0.05$ level in September 1994. The biomass of the first five management regimes was the production after the mowing in June. The biomass of the last four management regimes was not cut in June.

Table 55. Mean biomass in September per management regime in 1994. Homogeneous groups at $p<0.05$ level.

Management	Biomass ton/ha	Homogeneous groups
M+G	1.5	a . . .
2xM+r	1.8	a . . .
1xM+r-el	2.2	a . . .
2xM-r	2.2	a . . .
2xM+-r	2.8	a b . .
1xM+r/2y	4.1	. b c .
1xM+r-lt	4.5	. . c .
No manag	6.8	. . . d
Burning	6.9	. . . d

Table 56 shows the annual crop production of four management regimes in 1994 and the homogeneous groups at the $p<0.05$ level. In 1994 annual crop production was significantly smaller under hay-making in June with grazing in September (M+G) and hay-making twice a year than it was under mowing twice a year without removal of the mowings at least once (see table 56).

Table 56. Annual crop production per management regime in 1994. Homogeneous groups at $p<0.05$ level.

Management	Ann. prod. ton/ha	Homogen. groups
M+G	7.7	a .
2xM+r	8.2	a .
2xM+-r	9.8	. b
2xM-r	10.3	. b

Relation between above-ground biomass, N content in biomass and N mineralization in 1994

There appeared to be a positive correlation ($p<0.001$) between the peak standing crop and the nitrogen content in the biomass expressed as %. No correlation was found between the peak standing crop in June and the N mineralization between 28 March and 20 June, or between the N content in the biomass in June and the N mineralization.

5.3.4 N, P and K contents in the biomass and nutrient removal by management

Table 57 shows the N, P and K contents in the above-ground biomass per management regime in 1994. The N content at burning (1.83%) appeared to be significantly higher ($p<0.05$) compared with the other management regimes. The differences in P and K content were not significant at $p<0.05$.

Table 57. Mean N, P and K contents in above-ground biomass per management regime in 1994.

Management	N %	P %	K %
2xM+r	1.29	.21	1.48
2xM+-r	1.34	.20	1.40
2xM-r	1.19	.19	1.74
1xM+r-el	1.13	.18	1.23
1xM+r-lt	1.23	.19	1.25
1xM/2y-1	1.09	.19	1.39
M+G	1.33	.20	1.35
G+M	1.27	.19	1.71
2xG	1.28	.21	1.44
Gseas	1.47	.20	1.78
Burning	1.83	.16	1.30
No manag	1.38	.17	1.29

More than 50 kg N $ha^{-1}.yr^{-1}$ is actually removed by the management practices 2xM+r, 2xM+-r, 1xM+r-el and M+G (see table 58). Under 1xM+r-lt the amount of removed nitrogen was about equal to the nitrogen input by atmospheric deposition. Under 2xM-r and 1xM+r/2y nitrogen removal is less than the assumed atmospheric deposition and nitrogen probably accumulates.

Table 58. N removal per management.

Management	Biomass (kg/ha) June	Biomass (kg/ha) Sept.	N%	N removal (kg/ha) June	N removal (kg/ha) Sept.	Total (kg/ha)
2xM+r	6484	1770	1.29	83.64	22.83	106.47
2xM+-r	7075	2773	1.34	94.81	.00	94.81
2xM-r	8053	2243	1.19	.00	.00	.00
1xM+r-el	7495	2170	1.13	84.69	.00	84.69
1xM+r-lt	7021	4510	1.23	.00	55.47	55.47
1xM+r/2y	7848	4083	1.09	.00	22.26	22.26
M+G	6227	1490	1.33	82.82	.00	82.82

Except for 2xM-r, under all management practices the amount of removed phosphorus exceeds the phosphorus input by atmospheric deposition estimated between 0.3 and 1.7 kg $ha^{-1}.yr^{-1}$ (table 59).

Table 59. P removal per management.

Management	Biomass (kg/ha) June	Biomass (kg/ha) Sept.	P%	P removal (kg/ha) June	P removal (kg/ha) Sept.	Total (kg/ha)
2xM+r	6484	1770	0.21	13.62	3.72	17.34
2xM+-r	7075	2773	0.20	14.15	.00	14.15
2xM-r	8053	2243	0.19	.00	.00	.00
1xM+r-el	7495	2170	0.18	13.49	.00	13.49
1xM+r-lt	7021	4510	0.19	.00	8.57	8.57
1xM+r/2y	7848	4083	0.19	.00	3.88	3.88
M+G	6227	1490	0.20	12.45	.00	12.45

Assuming the atmospheric deposition of K to be between 10 and 20 kg $ha^{-1}.yr^{-1}$ with a mean value of 15 kg $ha^{-1}.yr^{-1}$ potassium is actually removed by all mowing regimes except by mowing twice a year without removal of the mowings (table 60). Under mowing once every two years potassium was only lost in the year of mowing. Measured over two years, the potassium that is actually removed nearly equals the amount of deposition in two years.

Table 60. K removal per management.

Management	Biomass (kg/ha) June	Biomass (kg/ha) Sept.	K %	K removal (kg/ha) June	K removal (kg/ha) Sept.	Total (kg/ha)
2xM+r	6484	1770	1.48	95.96	26.20	122.16
2xM+-r	7075	2773	1.40	99.05	.00	99.05
2xM-r	8053	2243	1.74	.00	.00	.00
1xM+r-el	7495	2170	1.23	92.19	.00	92.19
1xM+r-lt	7021	4510	1.25	.00	56.38	56.38
1xM+r/2y	7848	4083	1.39	.00	28.38	28.38
M+G	6227	1490	1.35	84.06	.00	84.06

N/P ratio in above-ground and below-ground biomass

The mean N:P ratio in above-ground biomass varied from 4.1 to 11.3. The mean N:P ratio in below-ground biomass varied from 6.6 to 10.9.

5.3.5 Vegetation pattern

Sheep prefer to graze on more or less flat parts of river dikes. On the steeper parts of the slopes they forage more selectively than on the flatter parts. It was especially on the steeper slopes that a mosaic of taller tufts interspersed with shorter turf emerged. The taller tufts ranged from 0.20 m to several metres in diameter. This mosaic is referred to as a micro-pattern. The heavily grazed areas had a canopy height less than 5 cm and hardly any litter accumulation; lightly grazed patches had a canopy height of more than 10 cm and more litter accumulation. The micro-pattern was first recorded three years after the reconstruction of the experimental river dike. Only then was a clear difference apparent between heavily and lightly grazed areas. The micro-pattern was clearest under grazing throughout the summer, with grazing twice a year in the second place, followed by grazing in spring and hay-making in autumn. Grazing in the early growing season seems to have an especially marked impact on creating a micro-pattern. There is plenty of food, so sheep can graze selectively. There is no need to forage less palatable species. Mowing in June with grazing in autumn revealed hardly any micro-pattern. Under mowing regimes the management intensity was equally high everywhere and no micro-patterns occurred.

Differences in species richness between the different methods of reconstruction were already apparent in the smallest area determined (i.e. 0.25 m^2) (see figure 25). The species richness in 1 m^2 in the spared zone and on replaced topsoil was already higher than it was in 24 m^2 in the other methods of reconstruction. Whereas the species richness in 24 m^2 was almost equal on replaced sods, replaced subsoil and imported clay, in 0.25, 1 and 4 m^2 it was significantly lower on imported clay.

Comparing the four most frequent mowing managements revealed a significantly highest species richness under hay-making twice a year (see figure 26). The significantly highest number of species had already appeared in the smallest determined surface area of 0.25 m^2. The species richness under hay-making twice a year was already higher in 4 m^2 than it was in 24 m^2 under the other management regimes.

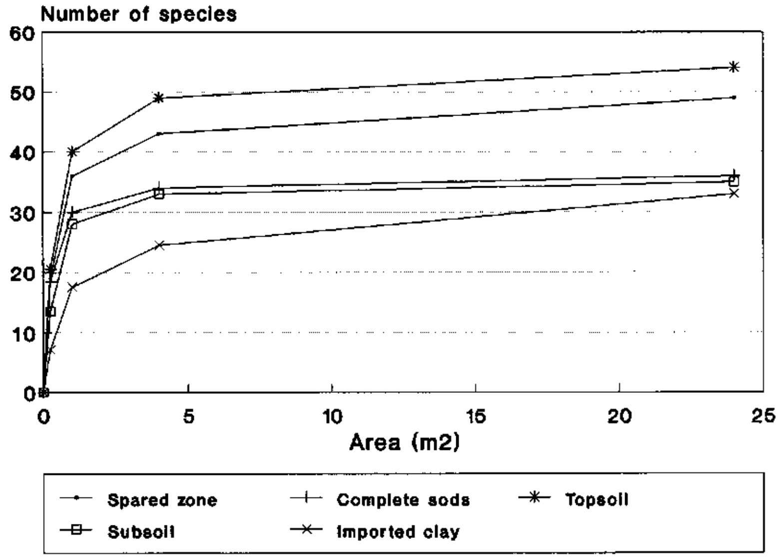


Figure 25. Relation between species richness and plot area per method of reconstruction under management hay-making twice a year in 1994.

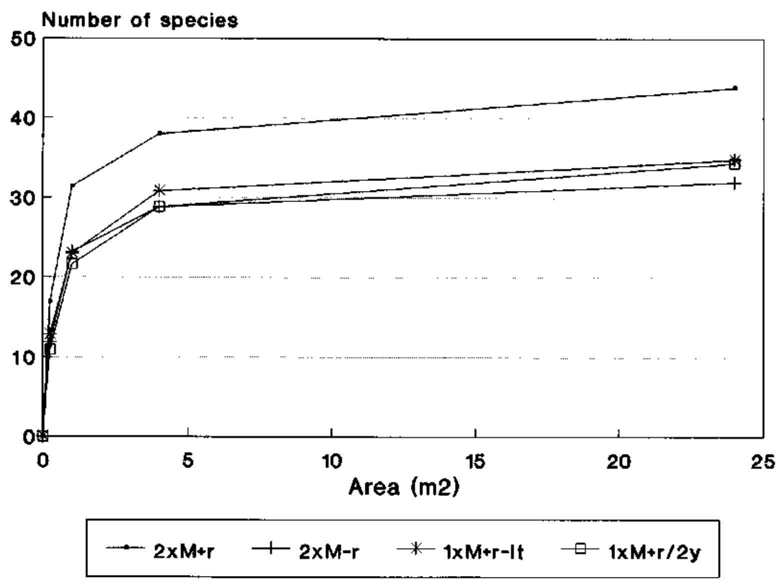


Figure 26. Relation between species richness and research area per management practice in 1994.

5.3.6 Canopy structure

In section C the largest peak standing crops were measured under mulching twice a year and under no management (figure 27).

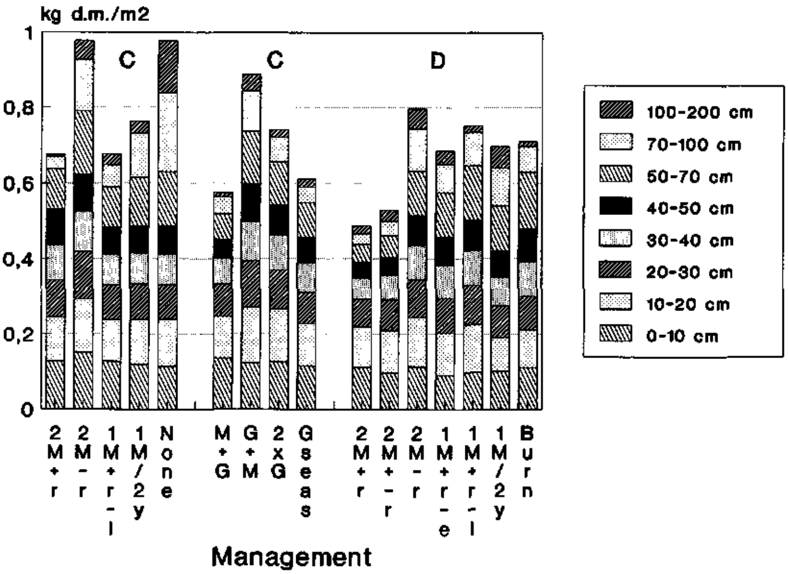


Figure 27. Proportional distribution of the biomass over the height per management practice in 1994. Replaced topsoil in sections C and D.

Whereas under no management the extra biomass production mainly came from plant parts above 70 cm, under mulching twice a year it also came from the 0-30 cm layer. In section D the differences in peak standing crop between hay-making twice a year and hay-making in June in combination with mulching in September on the one hand and on the other hand the other five management practices were mainly caused by larger biomass components above 50 cm. The peak standing crop under hay-making twice a year was larger in section C than in section D, obviously reflecting the difference in clay content, which was 36.4% in section C and 21.6% in section D.

5.3.7 Light penetration

Relation between amount of light and species richness
The number of species showed the highest positive correlations with far-red, green and total light ($p<0.001$) (see table 61).

*Table 61. Pearson correlation coefficients between different light parameters and species richness. Minimum pairwise N of cases: 74; 2-tailed significance: ** = $p<0.001$.*

Blue	.2283
Green	.4458**
Red	.3087
Far-red	.4703**
Red:far-red	.1750
Total light	.3978**

Table 62 shows relatively high light penetrations in the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) and the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) and a relatively low light penetration in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II).

Table 62. Mean penetration ($\mu mol.m^{-2}.s^{-1}$) of far-red and total light per plant community in 1994. Homogeneous groups at $p<0.05$ level.

Far-red light			*Total light*		
Plant comm.	Amount of light	Homogen. groups	Plant comm.	Amount of light	Homogen. groups
II	4.6629	a . .	II	1.2191	a .
I	5.2736	a b .	I	1.6074	a .
V	6.3961	. b .	V	2.2612	a b
VI	7.5643	. b c	VI	2.5136	a b
III	9.4128	. . c	III	3.3690	. b

Table 63 shows relatively high light penetrations under hay-making twice a year and low light penetrations under the burning regime, under mowing once every two years and under the grazing twice a year regime.

Table 63. Mean penetration ($\mu mol.m^{-2}.s^{-1}$) of far-red and total light per management strategy. Homogeneous groups at $p<0.05$ level.

Far-red light			*Total light*		
Management	Amount of light	Homogeneous groups	Management	Amount of light	Homoeneous groups
1xM+r/2y	3.8843	a . .	Burning	.6392	a . .
Burning	4.0101	a b .	1xM+r/2y	1.0930	a . .
2xG	5.0545	a b .	2xG	1.1186	a . .
Gseas	5.4722	a b .	Gseas	1.5270	a b .
No manag	5.8949	a b .	G+M	1.5963	a b .
2xM-r	5.9425	a b .	2xM-r	1.7091	a b .
G+M	5.9813	a b .	1xM+r-1t	1.9180	a b .
1xM+r-el	6.3037	a b .	M+G	1.9969	a b .
2xM+-r	6.6284	a b .	1xM+r-el	2.3241	a b .
1xM+r-1t	6.7066	. b .	2xM+-r	2.4460	a b .
M+G	7.2706	. b .	No manag	3.1881	. b c
2xM+r	10.9511	. . c	2xM+r	4.8247	. . c

5.3.8 Relation between above-ground biomass and species richness

In 1994 the number of herb species and grass species and the total number of species showed the highest negative correlations with the annual crop production (see table 64). These correlations were much higher than with peak standing crop in June and with biomass in September. From 40 to 50% of the species richness could be explained by annual crop production only.

*Table 64. Pearson correlations coefficients (r) and coefficients of determination (r^2 in %) between biomass in June and September, annual production, total number of species, number of grasses and number of herbs. Minimum pairwise N of cases: 29; 2-tailed significance: * = p<0.001.*

Correlations	Biom.June		Biom.Sept		Ann.prod.	
	r	r^2	r	r^2	r	r^2
N-species	-.47*	22	-.30	9	-.70*	50
N-grasses	-.23	5	-.32	10	-.63*	40
N-herbs	-.48*	23	-.26	7	-.66*	44

Figure 28 shows the relationship between the total number of species, the number of herbs and the number of grasses and the annual crop production. The lines are constructed by linear regression. The negative relation of biomass with the number of herb species is much more pronounced than with the number of grass species.

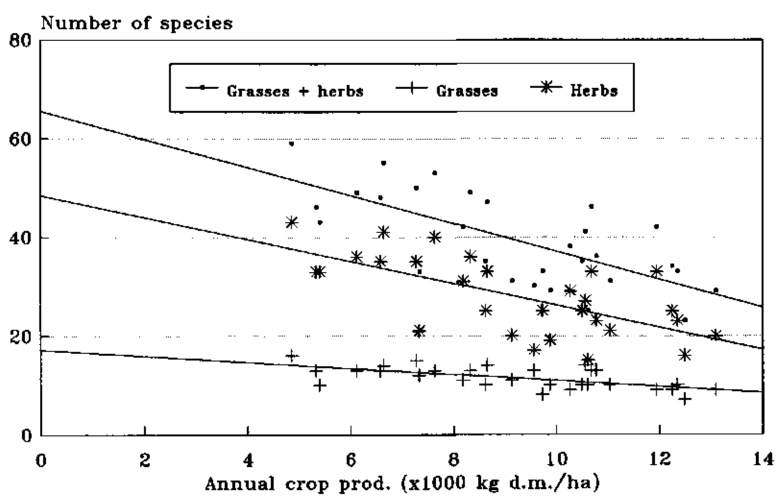


Figure 28. Relation between number of herbs, number of grasses and total number of species and annual crop production in 1994.

5.3.9 Relation between method of reconstruction, sowing and management and species richness

Method of reconstruction

In 1994 the mean species number in the spared zone, on replaced topsoil and on replaced subsoil was significantly higher than on imported clay (table 65). Because of the small number of permanent quadrats on complete sods the variation of the mean number of species was relatively high. For this reason differences with the other methods of reconstruction were not significant. The mean number of grass species on the imported clay was significantly lower than on the other methods of reconstruction. The mean number of herbs in the spared zone, on replaced topsoil and on replaced subsoil was significantly higher than on sods and on imported clay.

Table 66 shows the numbers of species of the four most frequent mowing practices in all methods of reconstruction in 1994. In 1994 the highest number of species in all methods of reconstruction was under hay-making twice a year, except on the replaced subsoil, where the number of species was very similar in all four management practices. The greatest difference in species number was between hay-making twice a year and mulching twice a year, especially in the spared zone and on the replaced topsoil.

The mean number of species was highest in the spared zone, followed by replaced subsoil. The number of species was lowest on complete sods and on imported clay. There were no significant differences between the methods of reconstruction. The mean number of species under hay-making twice a year was significantly higher than under the other mowing practices. On the replaced topsoil the number of species under hay-making twice a year was significantly higher than under the other management practices.

Table 65. Mean number of species per method of reconstruction in 1994. Homogeneous groups at $p<0.05$ level.

Method of reconstr.	Species number	Homogeneous groups
Herbs + Grasses		
Sp. zone	37.8	a .
Subsoil	36.4	a .
Topsoil	35.2	a .
Sods	32.0	a b
Imp. clay	31.1	. b
Grasses		
Sp. zone	12.1	a . .
Sods	11.0	a b .
Subsoil	10.7	a b .
Topsoil	10.5	. b .
Imp. clay	9.6	. . c
Herbs		
Subsoil	25.7	a .
Sp. zone	25.7	a .
Topsoil	24.7	a .
Imp. clay	21.5	. b
Sods	21.0	. b

Table 66. Number of species per method of reconstruction and per management in 1994.

Method of reconstruction	N	Management 2xM+r	1xM+r	1xM/2y	2xM-r	Mean
Spared zone	1	49.0	40.0	34.0	31.0	38.5
Complete sods	1	36.0	26.0	33.0	33.0	32.0
Replaced topsoil	10	42.6	33.3	33.2	29.0	34.5
Replaced subsoil	4	38.0	37.0	38.5	37.8	37.8
Imported clay	8	36.0	34.3	30.0	30.3	32.6
Total	24	39.6	34.2	33.0	31.1	34.5

Sowing

Table 67 shows the mean number of all species and the mean number of grass species per sowing. When sown with the locally gathered mixture (LGM) or the combination of the locally gathered mixture and *Lolium multiflorum* (LGM+Lm), the mean number of species was significantly higher ($p<0.05$) than when sown with the standard mixture BG5. Although not significant, species richness was higher when sown with LGM+D1 compared to only D1, and when sown with LGM+BG5 compared to only BG5. This suggests that adding LGM to the other sowings has a positive effect on species richness. However, comparing sowing LGM to sowing LGM+D1 and LGM+BG5 reveals that D1 and BG5 seem to weaken the positive effect on species richness of sowing with LGM. The negative effect of adding D1 seems to be greater than of adding BG5.

Table 67. Mean number of all species and mean number of grasses and herbs in 1994. Homogeneous groups at p<0.05 level.

Sowing mixture	N	Herbs + grasses	Homog. groups	Grasses	Herbs
LGM+Lm	14	38.2	a .	11.9	26.3
LGM	8	38.0	a .	9.6	28.4
LGM+BG5	7	36.3	a b	12.3	24.0
LGM+D1	120	34.2	a b	10.3	23.9
No sowing	35	33.4	a b	10.0	23.4
D1	9	31.4	a b	9.9	21.5
BG5	16	30.9	. b	10.2	20.7

Management

In 1994 the mean number of species under hay-making twice a year was significantly higher than under hay-making once every two years, mulching twice a year, grazing twice a year, no management, grazing in June in combination with hay-making in September, grazing throughout the summer and burning (table 68).

Table 68. Mean species number per management in 1994. Homogeneous groups at p<0.05 level.

Management	N	Mean species number	Homogeneous groups p<0.05
2xM+r	38	38.2	a .
M+G	16	35.8	a b
1xM+r-lt	34	35.0	a b
2xM+-r	10	34.7	a b
1xM+r-el	14	34.6	a b
1xM+r/2y	24	33.0	. b
2xM-r	28	32.6	. b
2xG	14	32.1	. b
No manag	3	31.7	. b
G+M	12	31.3	. b
Gseas	14	30.3	. b
Burning	2	26.5	. b

5.3.10 Relation between method of reconstruction and management and number of rare species

Methods of reconstruction

The sum of the proportions of the rare, fairly rare and less common species (i.e. respectively nrc classes 3, 4 and 5) was highest in the spared zone (7.1%) (see figure 29). The sum of the proportions of the rare to less common species was lowest in the replaced complete sods (0.6%). Also the proportion of the fairly common species (nrc class 6) was highest in the spared zone (2.7%). In contrast, the proportion of the extremely common species was relatively larger in the other methods of reconstruction.

Management

In 1994 the sum of the proportions of the rare, fairly rare and less common species (i.e. respectively nrc classes 3, 4 and 5) was highest under hay-making twice a year and under hay-making in June in combination with mulching in September (see figure 30). Under grazing throughout the summer and under the burning management hardly any rare to less common species were found. The proportion of the rare species (nrc 3) was largest under hay-making twice a year followed by hay-making once a year in September.

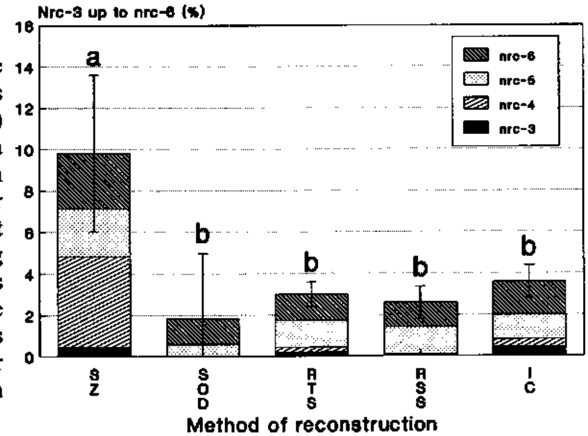


Figure 29. Proportions of the most important nrc classes per method of reconstruction in 1994.

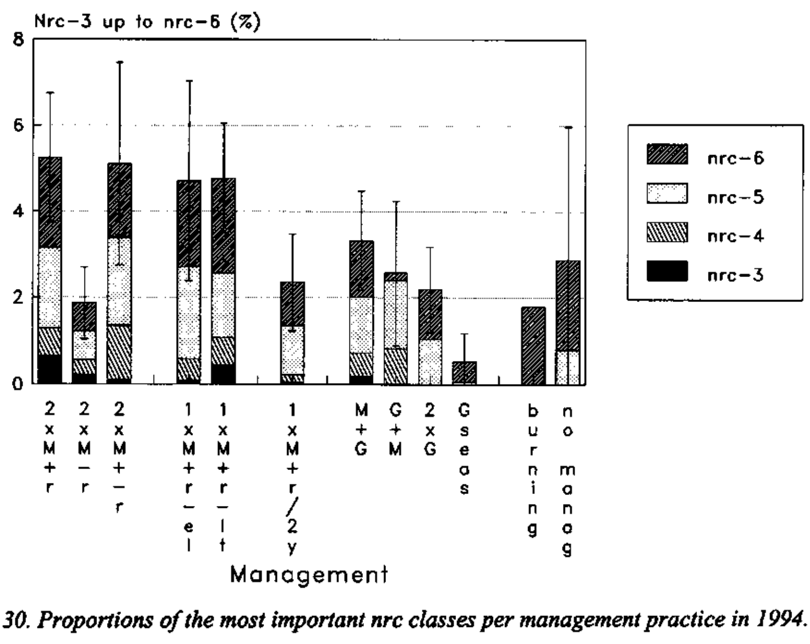


Figure 30. Proportions of the most important nrc classes per management practice in 1994.

5.3.11 Vegetation composition in 1994

The effect on the vegetation composition in 1994 of the method of reconstruction, sowing and management is described below.

Plant communities in 1994

In 1994 only 5 plant communities occurred frequently on the experimental river dike: the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I), the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II), the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III), the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) and the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI). The *Arrhenatheretum* with

Table 69. Synoptic table of the different methods of reconstruction. Both the exclusively differentiating species and the species that are differentiating for more than one method of reconstruction are boxed.

Method of reconstruction	SZ	SOD	RTS	RSS	IC
No. of relevés	11	4	96	33	65
Mean species no.	37.8	32.0	35.2	36.4	31.1
Standard deviation	5.0	3.7	9.0	5.4	8.0
Avenula pubescens	IV	II	II	+	I
Lamium album	V	II	I	I	II
Peucedanum carvifolia	IV	-	I	-	I
Rumex thyrsiflorus	V	-	I	-	I
Verbascum nigrum	IV	-	+	-	+
Calamagrostis epigejos	II	-	+	-	+
Centaurea jacea	V	III	IV	III	III
Rubus caesius	V	III	III	II	II
Valeriana officinalis	-	III	I	-	-
Cardamine pratensis	-	IV	+	-	+
Holcus lanatus	II	V	II	I	I
Polygonum amphibium	III	V	III	I	III
Rumex acetosa	I	V	IV	IV	III
Festuca arundinacea	III	V	III	III	II
Lysimachia nummularia	I	IV	III	III	+
Cichorium intybus	-	-	I	II	I
Crepis capillaris	I	-	I	III	I
Trifolium hybridum	-	-	I	IV	I
Medicago lupulina	II	-	III	V	II
Geranium dissectum	II	-	III	V	III
Trifolium dubium	II	-	III	V	III
Senecio jacobea	III	-	III	IV	II
Cerastium fontanum	III	-	II	II	II
Trifolium pratense	III	-	III	V	IV
Daucus carota	III	-	II	III	III
Allium vineale	IV	-	II	IV	II
Phleum pratense	IV	-	III	III	IV
Vicia sativa ssp.nigra	V	II	IV	V	IV
Glechoma hederacea	V	V	V	V	III
Galium mollugo	V	V	V	V	II
Veronica chamaedrys	II	IV	II	III	+
Achillea millefolium	IV	III	III	I	III
Equisetum arvense	III	II	II	-	II
Symphytum officinale	IV	V	IV	I	III

Leucanthemum vulgare and *Trifolium pratense* (IV) was represented by only 2 permanent quadrats, the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) by only 3 quadrats. The fragmentary community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion elatioris/Eu-Polygono-Chenopodion*] (VIII) and the fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) had disappeared. The plant communities are described in chapter 3.

Differential species per method of reconstruction in 1994

In table 69 the differential species per method of reconstruction are outlined. Not only the exclusively differential species are shown but also the species that are differential for more than one method of reconstruction. In the spared zone (SZ) 24 differential species are distinguished. Eight of them are exclusively differential; *Avenula pubescens, Calamagrostis epigejos, Centaurea jacea, Lamium album, Peucedanum carvifolia, Rubus caesius, Rumex thyrsiflorus* and *Verbascum nigrum*. *Rumex acetosa* is negatively differential. In 1987 *Calamagrostis epigejos, Peucedanum carvifolia, Rumex thyrsiflorus* and *Verbascum nigrum* only appeared in the spared zone. After 1987 they sparsely dispersed to bordering reconstructed parts of the experimental dike.

In the complete sods (SOD) 13 species are differential, of which 6 are exclusively differential; *Cardamine pratensis, Festuca arundinacea, Holcus lanatus, Polygonum amphibium, Rumex acetosa* and *Valeriana officinalis*. Negatively differential are *Allium vineale, Cerastium fontanum, Daucus carota, Geranium dissectum, Medicago lupulina, Phleum pratense, Senecio jacobea, Trifolium dubium, Trifolium pratense* and *Vicia sativa ssp. nigra*. On replaced topsoil (RTS) 17 differential species are distinguished; none of them is exclusively differential. On replaced subsoil (RSS) of the 17 differential species only *Cichorium intybus, Crepis capillaris* and *Trifolium hybridum* are exclusively differential. *Achillea millefolium, Equisetum arvense, Polygonum amphibium* and *Symphytum officinale* are negatively differential. On imported clay (IC) 13 species are differential; none of them is exclusively differential. *Glechoma hederacea, Galium mollugo* and *Veronica chamaedrys* are negatively differential.

Syntaxonomical elements per method of reconstruction

The methods of reconstruction differed most in the proportion of the *Arrhenatheretum elatioris*. In 1994 the proportion of characteristic species of the *Arrhenatheretum elatioris* was largest in the replaced complete sods and smallest on imported clay (see table 70). The proportions of the differential species of the *Koelerio-Corynephoretea* and the *Festuco-Brometea* and the characteristic species of the *Trifolion medii* were largest in the spared zone. In contrast, the proportion of species

Table 70. Proportions of the syntaxonomical elements per method of reconstruction with significance ($p<0.05$) in 1994. The same character after two values indicates no significant difference.

Syntaxonomical elements	Method of reconstruction: Spared zone	Complete sods	Repl. topsoil	Repl. subsoil	Imp. clay
Koel-Cor & Fest-Brom*	2.32 a	0.57 bc	0.67 b	0.20 c	0.34 c
Molinio-Arrhenatheretea	27.33 c	33.06 ab	32.36 b	35.32 a	32.04 b
Arrhenatheretum	27.94 a	29.67 a	25.32 a	24.86 ab	22.72 b
Lolio-Cynosuretum	10.48 ab	5.48 c	9.94 b	12.10 a	10.89 ab
Plantaginetea	3.79 b	2.62 b	4.93 b	5.56 b	8.00 a
Artemisietea	13.09 a	13.58 a	10.45 a	5.58 b	9.75 a
Trifolion medii	0.87 a	0.40 ab	0.24 b	0.00 c	0.17 bc
Chenopodietea	2.84 b	3.66 ab	3.48 b	3.15 b	4.47 a
Other	11.34 b	10.98 b	12.60 ab	13.22 a	11.63 b

* = Koelerio-Corynephoretea & Festuco-Brometea (diff. species)

characteristic of the *Plantaginetea* was highest on imported clay whereas these plants of trampled areas only accounted for a small proportion in the spared zone. The proportion of characteristic species of the *Lolio-Cynosuretum* was largest on replaced subsoil and smallest in the replaced complete sods. The proportion of nitrophilous tall herbs assigned to the *Artemisietea* was largest on the replaced complete sods and smallest on replaced subsoil. The proportion of the annual pioneer species of the *Chenopodietea* was largest on imported clay and smallest in the spared zone.

Syntaxonomical elements per management regime
Figure 31 shows the proportions of the most important syntaxonomical elements. The proportion of the nitrophilous tall herbs assigned to the *Artemisietea* shows the largest variation. The largest proportion was found under burning and no management. Hay-making twice a year and the four grazing practices led to the smallest proportion of the *Artemisietea* species. The largest proportion of the species characteristic of the *Arrhenatheretum* was found under hay-making in June in combination with mulching in September. Grazing throughout the summer led to the smallest proportion of *Arrhenatheretum* species but, in contrast, to the largest proportion of species characteristic of the *Lolio-Cynosuretum*. The proportion of plants of trampled areas assigned to the *Plantaginetea* was largest under grazing throughout summer but also under grazing twice a year and grazing in June in combination with hay-making in September.

Effect of the management regime on the species abundance
The effect of the management regime was determined for all species in 1994. Figures 32 to 35 show the abundance of several species per management in 1994. The two most important grass species are *Arrhenatherum elatius* and *Lolium perenne*. *Arrhenatherum elatius* was favoured by mowing practices, whereas *Lolium perenne* was favoured by grazing (see figure 32). Grazing throughout the summer led to the lowest abundance of *Arrhenatherum elatius* but to the highest abundance of *Lolium perenne*. Under the burning practice and under no management *Lolium perenne* had disappeared in 1994, but *Arrhenatherum elatius* is still abundant. *Elymus repens* was favoured by the most extensive management practices 'no management', burning and hay-making once every two years. It was suppressed by grazing practices. *Trisetum flavescens* was slightly favoured by hay-making twice a year, hay-making once a year in September and hay-making in June in combination with grazing in the autumn.

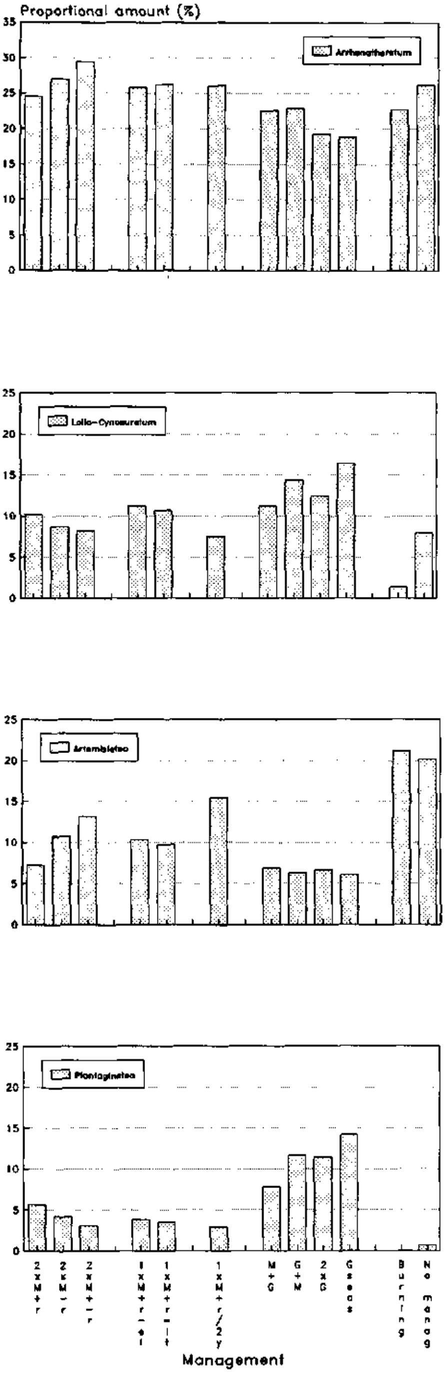


Figure 31. Proportions of the most important phytosociological elements of the management practices in 1994.

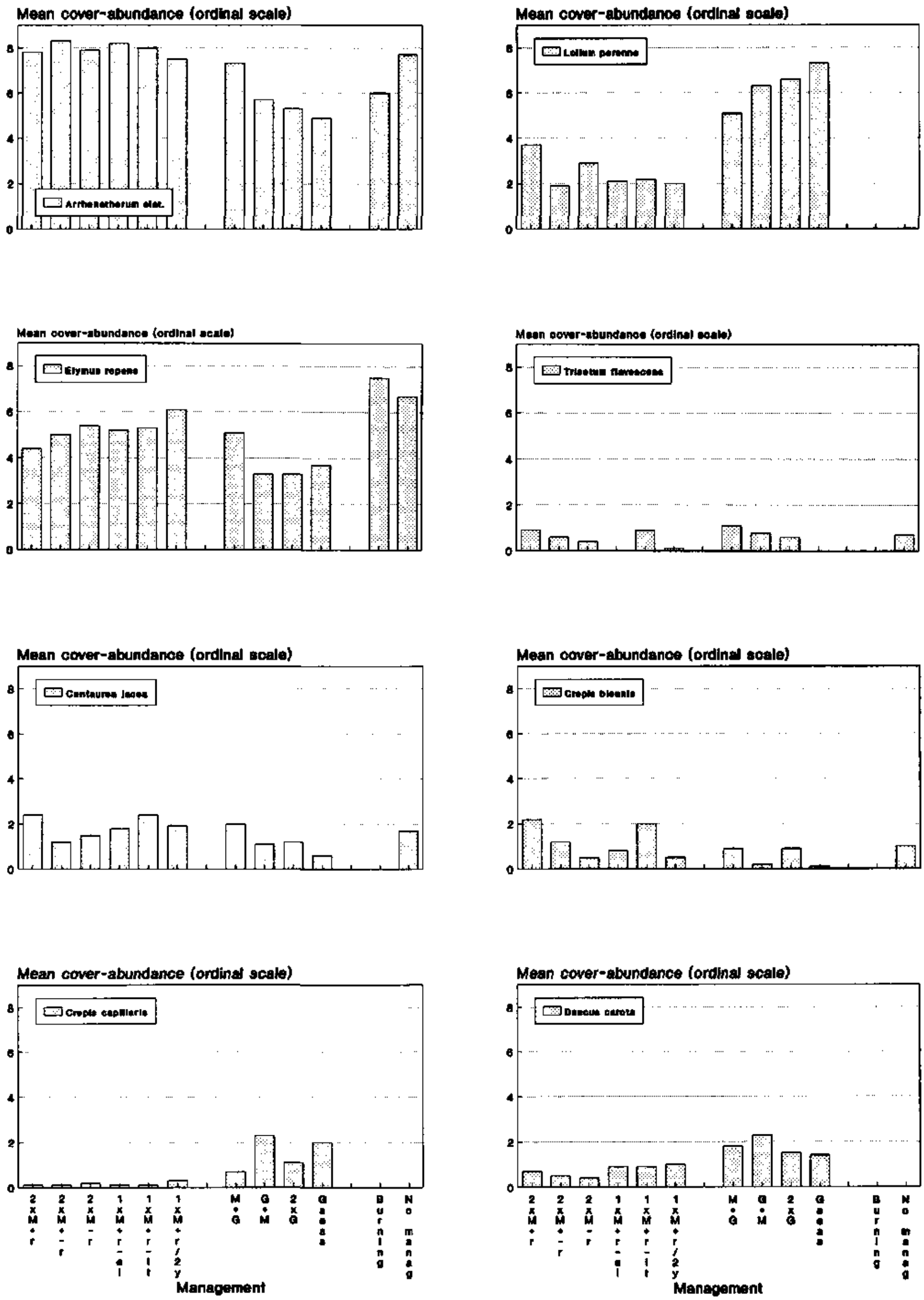


Figure 32. Mean cover-abundance of Arrhenatherum elatius, Lolium perenne, Elymus repens, Trisetum flavescens, Centaurea jacea, Crepis biennis, Crepis capillaris and Daucus carota per management regime in 1994.

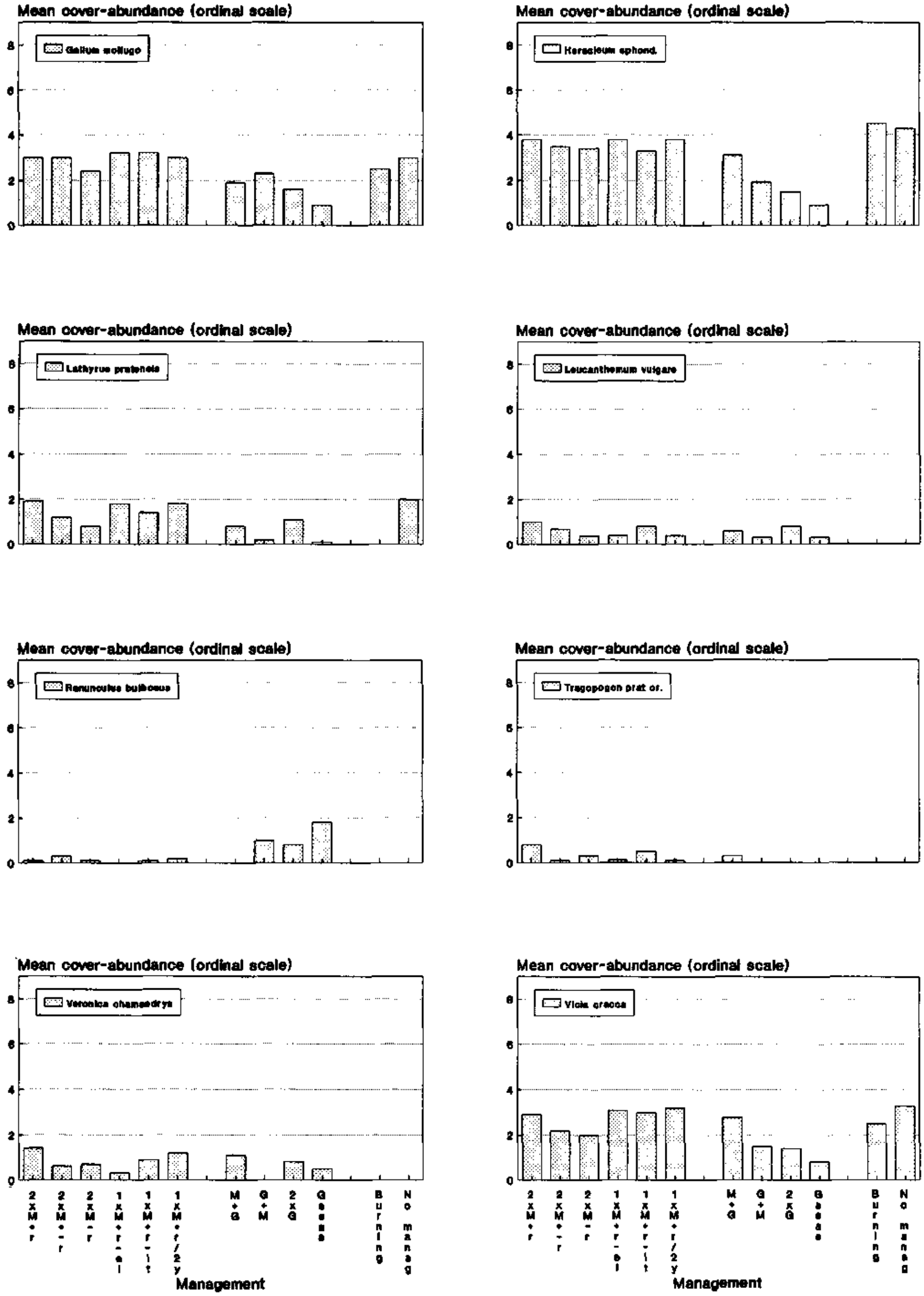


Figure 33. Mean cover-abundance of Galium mollugo, Heracleum sphondylium, Lathyrus pratensis, Leucanthemum vulgare, Ranunculus bulbosus, Tragopogon pratensis ssp. orientalis, Veronica chamaedrys and Vicia cracca per management regime in 1994.

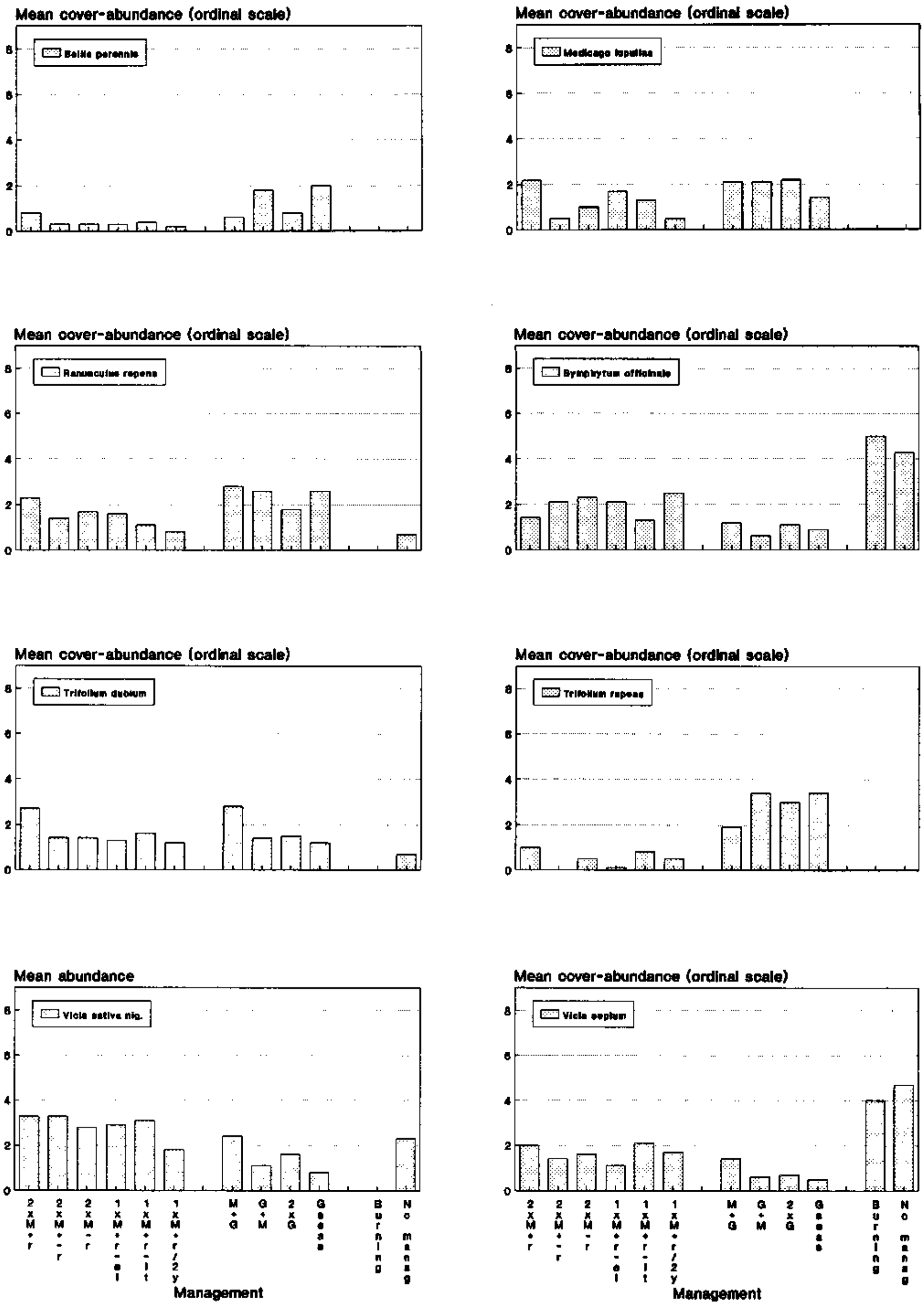


Figure 34. Mean cover-abundance of Bellis perennis, Medicago lupulina, Ranunculus repens, Symphytum officinale, Trifolium dubium, Trifolium repens, Vicia sativa ssp. nigra and Vicia sepium per management regime in 1994.

Centaurea jacea, Crepis biennis, Galium mollugo, Heracleum sphondylium, Lathyrus pratensis, Tragopogon pratensis ssp. orientalis, Vicia cracca and *Vicia sativa ssp. nigra* were favoured by mowing practices (see figure 32 to 34). *Crepis capillaris, Daucus carota, Ranunculus bulbosus, Bellis perennis, Medicago lupulina, Ranunculus repens* and *Trifolium repens* took advantage of the grazing practices. *Leucanthemum vulgare, Veronica chamaedrys* and *Trifolium dubium* showed no evident preference, except that they did hardly occur under burning and no management. *Symphytum officinale* and *Vicia sepium* were favoured by burning and no management.

Three of the four unwanted species were favoured by the relatively extensive management practice burning and no management: *Cirsium arvense, Rubus caesius* and *Urtica dioica* (see figure 35). *Cirsium arvense* was favoured also slightly by the grazing practices. *Cirsium vulgare* was favoured only by the grazing practices, especially by grazing throughout the summer and by grazing twice a year.

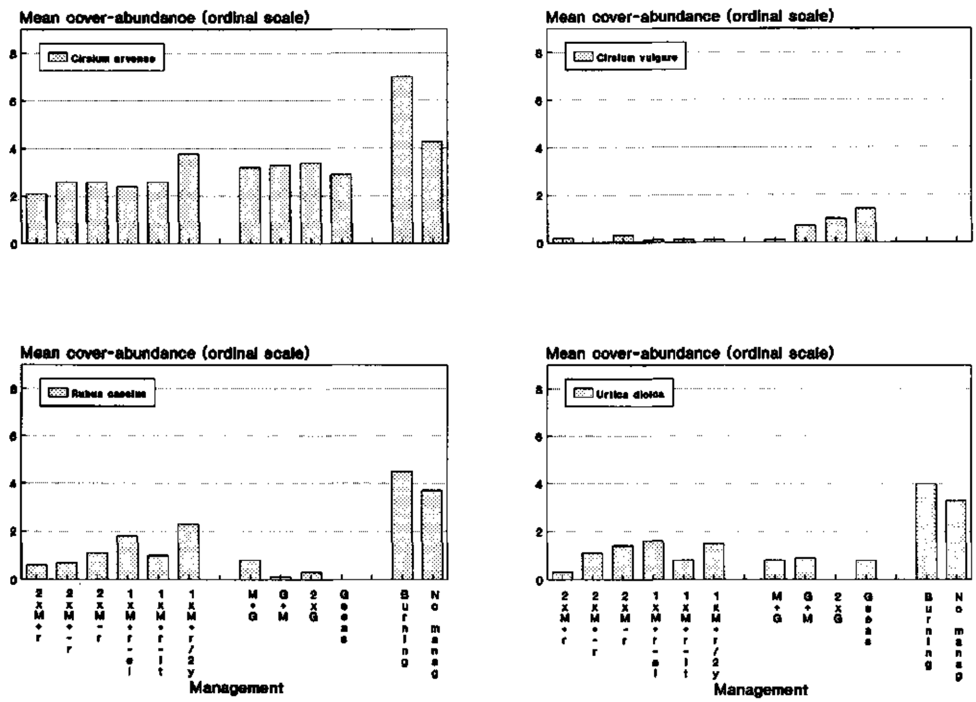


Figure 35. Mean cover-abundance of Cirsium arvense, Cirsium vulgare, Rubus caesius and Urtica dioica per management regime in 1994.

5.4 DISCUSSION

Germination and seedling establishment is influenced by a variety of environmental factors (see e.g. Silvertown, 1980, 1981; Fenner, 1987; Masuda & Washitani, 1990). Furthermore, the canopy structure of the vegetation, which determines both light penetration to the soil surface and microclimate, seems to be an important determinant of the onset of germination and seedling establishment (Oomes & Elberse, 1976; Verkaar *et al.*, 1983; Fenner, 1985; Goldberg, 1987). The canopy structure is especially influenced by the soil characteristics and the management regimes. Therefore, the impact of the soil characteristics and the management is of great importance to the re-establishment of species-rich grasslands on river dikes.

5.4.1 Plant communities

Soil characteristics

The vegetation composition on Dutch river dikes is greatly determined by the contents of clay, lime and nitrogen (Sýkora & Liebrand, 1987; Van der Zee, 1992). There is a large variation in the physical and chemical attributes of the soil of the experimental dike. Because of this heterogeneity it is to be expected that the ultimate vegetation on the whole experimental dike will not be homogeneous.

On the basis of the granular composition, especially the clay content, predictions can be made about which vegetation types can be expected on dikes when management is optimal (Sýkora & Liebrand, 1987; Van der Zee, 1992). At higher clay contents the role of the management will be greater for restoring species-rich grasslands than at lower clay contents (Berendse *et al.*, 1994). In general, higher clay contents lead to a larger above ground biomass which makes competition between species crucial with regard to the ultimate vegetation composition. At lower clay contents the biomass production is less which makes the competition between species, especially for light, less extreme. On the experimental dike the clay content varies from 16% to 38%. This indicates that plant communities that prefer soils with low clay content cannot be expected. For this reason the *Medicagini-Avenetum centaureetosum scabiosae* (Van der Zee, 1992) cannot be expected (clay: 3-10%) whereas the two variants of the *Arrhenatheretum* subass. group B *brizetosum*; the variant with *Galium verum* and *Pimpinella saxifraga* (clay: 5-18%) and the variant with *Galium verum* and *Agrostis capillaris* (clay: 5-20%) are less likely to occur. In principle, all other plant communities described by Van der Zee (1992) and occurring on river dikes might possibly develop in future, but only if the species can arrive via natural dispersion and if management is optimal (see appendix 2 on page 154).

The mean clay content of the soil under the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) was significantly lower than of the other communities. On the other hand, the mean clay content of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III), the second best developed plant community after the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I), was the highest. Obviously, the differences in clay content were too small to exert an unambiguous influence on the vegetation composition, except in the case of the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I). Moreover, the lime content of the soil under this community was higher than under all the other communities.

Relation between peak standing crop and annual production

Previous researchers have used both peak standing crop and annual biomass production to study the relation between species richness and the biomass production (Grime, 1979; Willems, 1980; Schiefer, 1983; Fliervoet, 1984; Bakker, 1989). It is not always clear if the biomass data presented by these authors concern peak standing crop (single yield of maximum biomass) or the annual biomass production (i.e. yields in June and September) (Van der Zee, 1992). Altena and Oomes deal with annual production and assume a maximum annual production of 5 to 6 ton $dw.ha^{-1}.yr^{-1}$ for species-rich grasslands (Altena & Oomes, 1985; Oomes, 1988, 1990). Calculations by Oomes (1992) show a peak standing crop which consists of 62% (± 5%) of the annual production. Based on the biomass data of all permanent plots with management mowing twice a year (with or without removal of the mowings) a clear increase of the ratio peak standing crop:annual production was measured in the present research between 1988 and 1994; 1988: 56.9%, 1989: 64.4%, 1990: 67.8%, 1992: 87.2%, 1994: 78.1%. Except for 1992, this increase could be explained by the shift of the main growth of the vegetation towards early summer. The high ratio in 1992 can be attributed to the large precipitation deficit in the summer period. Thus, the peak standing crop not only increased between 1987 and 1994 but was also reached earlier in the season every year. It seems probable that the development of the root system of the plants is important in these changes in vegetation dynamics.

In 1994 the ratio of peak standing crop:annual production in the plant communities was as follows: *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I): 83.9%, *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II): 73.5%, *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III): 77.6%, *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V): 69.1%, *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI): 77.5%. The proportion of the biomass in June is important when management is aimed at impoverishment of the soil. If this proportion is large, there is a high rate of nutrient removal with hay-making in June but a much lower removal of nutrients with hay-making in September.

Relation between above-ground biomass and species richness

In general, the highest species richness is found when the peak standing crop including litter is between 3.5 and 7.5 tons $dw.ha^{-1}.yr^{-1}$ (Al-Mufti *et al.*, 1977; Peet *et al.*, 1983). In comparison with the annual production of 5 to 6 ton $dw.ha^{-1}$ (dw = dry weight) assumed by Altena and Oomes (1985) and Oomes (1988, 1990) the annual production of the communities distinguished on the experimental dike was relatively high. In species-rich *Lolio-Cynosuretum* grasslands (40 species per 25 m^{-2}) Van der Zee (1992) measured a peak standing crop of 5.2 ton $dw.ha^{-1}$ and in species-rich *Arrhenatheretum* grasslands (35 species per 25 m^{-2}) 6.2 ton $dw.ha^{-1}$. Taking the highest estimation of Oomes (i.e. peak standing crop = 67% * annual production) as a starting point, the annual production of the species-rich *Lolio-Cynosuretum* and *Arrhenatheretum* grasslands was respectively 7.7 and 9.2 ton $dw.ha^{-1}$. These values are also relatively high. Van der Zee (1992) conjectured that on dike slopes production is higher than on flat grasslands. Taking the peak standing crop:annual production rates in 1994 of respectively the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) (77.5%) and the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) (77.6%) as a starting point, the annual production of the species-rich *Lolio-Cynosuretum* and *Arrhenatheretum* grasslands distinguished by Van der Zee (1992) was respectively 6.7 and 8.0 ton $dw.ha^{-1}$. These values suggest that the prospects are good for a further increase of the species richness of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III), which had an annual production of 7.6 ton $dw.ha^{-1}$, and of the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI), which had an annual production of 8.0 ton $dw.ha^{-1}$. By comparison, the annual production of the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) (8.7 ton $dw.ha^{-1}$) was intermediate. The high biomass production in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) and the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) will inhibit a high species richness. Species richness in these communities will probable further decrease in the future.

In 1994 the total number of species was negatively correlated ($p<0.001$) with the above-ground biomass in June. The negative relation of biomass with the number of herb species was much more pronounced than with the number of grass species. The total number of species, the number of herbs and the number of grasses were all negatively correlated ($p<0.001$) with the annual production. In this study the highest species diversity (59 species per 24 m^{-2}) was found at a peak standing crop of 3.5 ton $dw.ha^{-1}$. Bakker (1989) found the highest species diversity (≥ 20 species per 4 m^{-2}) between 2 and 4 ton $dw.ha^{-1}$, which is not in agreement with Grime's optimum of between 5 and 6 ton $dw.ha^{-1}$. Oomes & Mooi (1981; 1989) found that the species diversity did not always increase despite a large decrease of the standing crop. Immigration of species into a stand depends not only on the habitat conditions but also on the reservoir of species in the vicinity. But even if all conditions are optimal, it takes time before the developing vegetation communities are saturated. The question is whether this will occur at all, given the present state of increasing fragmentation of seed source areas.

Numerous alternative explanations for the effects of productivity on diversity have been proposed. Grime (1973, 1979), for instance, suggested that productive habitats have lower diversity because of more intense competition. Newman (1973) countered that competition is equally strong in both fertile and infertile habitats, but that in productive habitats strong competition for light inherently favors the tallest species, whereas in infertile habitats many alternative traits confer competitive ability for nutrients and thus allow numerous species to coexist. MacArthur & Wilson (1967) suggested that the biodiversity of a site depends on the interplay of local colonization (gain) and extinction (loss) rates. Tilman (1993) supposed that changes in species richness along productivity gradients should depend on the effects of productivity on both the colonization and extinction probabilities of species. In his study, experimental increases in productivity via nitrogen addition generally led to decreased species richness. The decreased diversity was caused as much by lower rates of species gain as by greater rates of loss of existing species. He concluded that diversity is lower in productive grasslands because accumulated litter, and possibly lower light penetration, inhibit germination and/or survival of seedlings, and thus decrease rates of establishment by new species. Higher productivity also leads to higher rates of loss of existing species, presumably via competitive displacement.

Attributes limiting biomass production

Three soil attributes which can limit biomass production are nitrogen, phosphorus and potassium. These elements must be present in a certain ratio to achieve optimal production. Manuring recommendations are usually attuned to these ratios. If one of these elements is deficient, biomass production can be limited. In practice, nitrogen and potassium appear to be the most important limiting elements whereas only in very rare circumstances phosphorus is limiting. Oomes (1988, 1990) contended that on sandy soils the attribute limiting biomass production is potassium and on clayey soils it is nitrogen. The soils in the fluviatile district are mostly intermediate between sandy and clayey soils. Both nitrogen and potassium can be the limiting attribute. In these circumstances only manuring research can show which element is limiting biomass production.

In unmanured grasslands fertility depends on the speed of mineralization of organic matter (Dickinson, 1984; Vaughn *et al.*, 1986). The decomposition of the organic matter greatly depends on the C/N ratio and the moisture content of the soil (Scheffer & Schachtschabel, 1976). Usually, the C/N ratio of soils with stabilized humus is about 10, but values of 8 and 9 are also possible (Janssen & Verveda, 1983). A C/N ratio higher than 12 or 13 indicates a N deficiency in the soil. This retards the humification process and thus the nitrogen mineralization. The C/N ratio of the organic matter in sandy soils is higher than in more clayey soils. On the experimental dike the mean C/N ratio per method of reconstruction never exceeded 12, which means that mineralization was never inhibited. On imported clay this ratio was exactly 12, so here further impoverishment might lead to N deficiency.

Relation between above-ground biomass, N content in biomass and N mineralization

In this study no relation could be distinguished between the peak standing crop in June and the annual production and the N mineralization between 28 March and 20 June. Neither could any relation be found between the N content in the biomass in June and the N mineralization between 28 March and 20 June. Similar findings are reported in the literature. Whereas the increase in the ratio between species indicating nutrient-poor and nutrient-rich soil conditions clearly indicated that some changes had taken place, which was confirmed by the decline of the above-ground standing crop, Bakker (1989) could not demonstrate the impoverishing of the soil from chemical analyses of soil from the reclaimed grassland area of the Westerholt or from the valley grasslands of Loefvledder. Oomes & Mooi (1981), Elberse *et al.* (1983) and Willems (1983a) recorded similar findings. Olff *et al.* (1994) also found that peak standing crop prior to cutting did not correspond to the annual nitrogen mineralization rate.

From their study of long-term effects of several cutting treatments on roadside vegetation Parr & Way (1988) concluded that removing cuttings led to a decrease in extractable potassium in the soil but most other soil nutrients, including total and available nitrogen, were unaffected. They suggest that the increase in species richness was not due to reduced levels of soil nutrients, but was probably associated with the disturbance and scarification which accompanied the removal of cuttings by mechanical raking, and with the alleviation of the smothering effect caused by leaving cut vegetation on the verges. The scarification caused by mechanical raking may be sufficient to create gaps in the surface layer of decumbent plants and thatch, exposing dormant seeds to the light and stimulating germination (Wesson & Wareing, 1969).

N/P ratio in above-ground and below-ground biomass

The N/P ratio of both above-ground and below-ground biomass indicate nitrogen to be limiting biomass production. In already unproductive grasslands Oomes (1990) measured N, P and K concentrations in dry matter: N 1.70% (±0.04); P 0.16% (±0.01) and K 1.01% (±0.03). In the present study the mean N yield in all management regimes was 1.27%, which supports the conclusion that N limits grassland production on the experimental river dike. The mean P and K yields were respectively 0.19% and 1.47% which reinforces this conclusion. Only under the burning regime are the relatively high N yield (1.83%) and the relatively low P yield (0.16%) likely to show that P limits biomass production. In cases of grassland restoration where N is the limiting factor for grassland production, attention must be paid to the input of N into the system.

5.4.2 Methods of reconstruction

Syntaxonomical elements

In 1994 the methods of reconstruction differed most in the proportion of the *Arrhenatheretum elatioris*. The proportion of characteristic species of the *Arrhenatheretum elatioris* was largest in the replaced complete sods and smallest on imported clay. The proportion of differential species of the *Koelerio-Corynephoretea* and the *Festuco-Brometea* and the proportion of the characteristic species of the *Trifolion medii* were highest in the spared zone.

In contrast, the proportion of species characteristic of the *Plantaginetea* was largest on imported clay whereas these plants of trampled areas only accounted for a small proportion in the spared zone. The proportion of characteristic species of the *Lolio-Cynosuretum* was largest on replaced subsoil and smallest in the replaced complete sods. The proportion of nitrophilous tall herbs assigned to the *Artemisietea* was largest on the replaced complete sods, due to the relative high clay content, N-mineralization and CN-ratio, and smallest on replaced subsoil. Finally, the proportion of the annual pioneer species of the *Chenopodietea* was largest on imported clay and smallest in the spared zone.

Species rarity

In 1994 the sum of the proportions of the rare, fairly rare and less common species (i.e. respectively nrc classes 3, 4 and 5) was highest in the spared zone (7.1%). In the other four reconstruction methods the sum of the proportions of these species was highest on imported clay (2.0%) followed by replaced topsoil (1.7%) and lowest in the replaced complete sods (0.6%). The proportion of the rather common species (nrc class 6) was also largest in the spared zone (2.7%) whereas in the other methods of reconstruction it varied from 1.2% to 1.6%. In contrast, the proportion of the extremely common species was relatively larger in the other methods of reconstruction than it was in the spared zone.

Relation between method of reconstruction, soil characteristics and above-ground biomass

All methods of recontruction appeared to have different soil characteristics. In the spared zone the clay content was relatively low and the sand content relatively high. The lime content was the highest whereas also the organic matter content was relatively high. The potassium and sodium contents were low whereas the calcium content was high. The complete sods differed most from the other methods of reconstruction. Their clay content was relatively high and the sand content relatively low. The soil fertility was the highest of all methods of reconstuction for the electrical conductivity and the contents of nitrogen, phosphorus and potassium were the highest. The organic matter content was also relatively high. The $CaCO_3$ content was the lowest of all methods of reconstruction. The organic matter content of the replaced subsoil was relatively low. The sodium content was the highest of all methods of reconstruction whereas the calcium content was the lowest. The lime content of the imported clay was relatively high. The clay content was relatively low and the sand content relatively high. The electrical conductivity was the lowest of all methods of reconstruction whereas also the contents of organic matter, nitrogen, phosphorus and sodium were relatively low. All physical and chemical attributes of the replaced topsoil were intermediate. In contrast with the lime content, the acidity of all methods of reconstruction was almost equal.

The relatively great differences in soil characteristics of the methods of reconstruction will probably lead to differences in the composition and structure of the ultimate vegetation on the different methods of reconstruction (Grime, 1979; Huston, 1979; Tilman, 1988). Generally, soils with a higher clay content will be more fertile than soils with a lower clay content. The clay content is positively correlated to the electrical conductivity, the organic matter content, the total nitrogen content, the potassium content and the C/N quotient, and negatively correlated to the sand content, the acidity, the lime content and the calcium content. A higher fertility causes a greater biomass production (Sýkora & Liebrand, 1987; Van der Zee, 1992). In nutrient-rich situations with a high biomass production only tall-growing plant species that are highly competitive are able to survive (Janiesch, 1973; Huston, 1979; Dierschke & Vogel, 1981). In these circumstances competition is for light more than for nutrients. Smaller species are unable to survive at high biomass production (Aperdannier, 1959; Yemm & Willis, 1962; Harper, 1970). Thus, the clay content will strongly influence the vegetation composition by means of the biomass which is highly correlated with the clay content and soil fertility (Marschall, 1966; Thurston, 1969; Rorison, 1970; Van der Maarel, 1971; Dirven & Neuteboom, 1975; Silvertown, 1980, Elberse *et al.*, 1983) .

Because biomass is strongly affected by management, only permanent plots under hay-making twice a year were considered when comparing the different methods of reconstruction. In 1990 the highest biomass in June was measured on the replaced complete sods (6.4 ton $dw.ha^{-1}$) and the lowest on the replaced subsoil (5.0 ton $dw.ha^{-1}$). In 1994 the highest biomass in June was again measured on the replaced complete sods (8.4 ton $dw.ha^{-1}$) and the lowest biomass was now measured on the replaced topsoil (5.7 ton $dw.ha^{-1}$). Between 1990 and 1994 the peak standing crop on all methods of reconstruction increased. On complete sods it increased from 6.4 to 8.4 ton $dw.ha^{-1}$, on replaced subsoil from 5.0 to 7.2 ton $dw.ha^{-1}$ and on imported clay from 5.2 to 7.1 ton $dw.ha^{-1}$. On replaced topsoil and in the spared zone the increase was much smaller: respectively from 5.3 to 5.7 ton $dw.ha^{-1}$ and from 5.9 to 6.7 ton $dw.ha^{-1}$. This indicates that in 1990 the vegetation on the replaced subsoil and imported clay was less far developed than the vegetation on the other methods of reconstruction. The vegetation was unable to optimally take up the available nutrients. One reason for this could be that the root system was not optimally developed at that moment, possibly because the soil was too compact directly after the reconstruction. In 1994 the root systems had developed and production had increased. The increase of production on replaced sods might be caused by the roots penetrating soil directly beneath. In addition, the clay content, the N-mineralization and the CN-ratio of the complete sods appeared to be relatively high and, as these are positively correlated with the soil fertility, this could explain the increase in production. In 1994 the annual production under hay-making twice a year was largest on replaced complete sods (10.8 ton $dw.ha^{-1}$) and smallest on replaced topsoil (7.6 ton $dw.ha^{-1}$).

5.4.3 Sowing

Relation between sowing and above-ground biomass

Because biomass is strongly affected by management, only permanent plots with management haymaking twice a year were considered when comparing the different sowings. In 1990 the peak standing crop of sowing with D1+LGM was significantly larger compared with sowing with BG5, LGM and D1. Besides, the peak standing crop under 'no sowing' was significantly larger compared with sowing with BG5. It is concluded that sowing with BG5 retards the development of the vegetation in the direction of species-rich grassland; the production achieved is smaller compared with the other sowings. The sowing density is important in this. The higher the sowing density, the more the development is retarded. Sowing with D1, used in low density, in combination with LGM gave the fastest development of the vegetation. In 1994 the highest biomass in June was on permanent plots with no sowing and the lowest biomass on permanent plots with sowing BG5+LGM. In 1994 the differences between the sowings were smaller than in 1990. Whereas in the first years after the reconstruction the method of reconstruction and the sowing were the most important factors, in 1992 and 1994 the management was becoming more and more important.

5.4.4 Management

Syntaxonomical elements

The changes in vegetation composition and structure can be clearly related to management practices. In 1994 the proportion of the nitrophilous tall herbs assigned to the *Artemisietea* showed the largest variation. The largest proportion was found under burning and no management. Hay-making twice a year and the four grazing practices led to the smallest proportion of the *Artemisietea* species. The largest proportion of the species characteristic of the *Arrhenatheretum* was found under hay-making in June in combination with mulching in September. Grazing throughout the summer led to the smallest proportion of *Arrhenatheretum* species but, in contrast, to the largest proportion of species characteristic of the *Lolio-Cynosuretum*. The proportion of plants of trampled areas, assigned to the *Plantaginetea*, was largest under grazing throughout the summer but also under grazing twice a year and grazing in June in combination with mowing in September. These results are in accordance with Sýkora *et al.* (1990) who also showed that even changes at the low level of syntaxonomic hierarchy, i.e. sub-associations and variants, can be understood in terms of management practices.

Species composition

Both grass species and herb species are affected by the management applied. In 1994, *Arrhenatherum elatius* was the most abundant grass species at the mowing practices whereas *Trisetum flavescens* was also slightly favoured by hay-making. At the grazing practices *Lolium perenne* was the most abundant grass species. *Elymus repens* was favoured by the most extensive management practices 'no management', burning and hay-making once every two years. It was suppressed by grazing practices. Under the burning practice and under no management *Lolium perenne* disappeared, but *Arrhenatherum elatius* was still abundant in 1994. *Centaurea jacea, Crepis biennis, Galium mollugo, Heracleum sphondylium, Lathyrus pratensis, Tragopogon pratensis ssp. orientalis, Vicia cracca* and *Vicia sativa ssp. nigra* are favoured by mowing practices. *Crepis capillaris, Daucus carota, Ranunculus bulbosus, Bellis perennis, Medicago lupulina, Ranunculus repens* and *Trifolium repens* took advantage of the grazing practices. *Leucanthemum vulgare, Veronica chamaedrys* and *Trifolium dubium* showed no evident preference, except that they did hardly occur under burning and no management. *Symphytum officinale* and *Vicia sepium* were favoured by burning and no management.

Three of the four unwanted species were favoured by the relatively extensive management practice burning and no management: *Cirsium arvense, Rubus caesius* and *Urtica dioica*. *Cirsium arvense* was slightly favoured also by the grazing practices. *Cirsium vulgare* was favoured only by the grazing practices, especially by grazing throughout the summer and by grazing twice a year. The finding of *Elymus repens* being abundant on a river dike, whether or not in combination with *Cirsium arvense, Rubus caesius* or *Urtica dioica*, indicates a relatively extensive management whereas the the above-ground biomass will be high and the species richness will probably be low .

Species rarity

In 1994 the sum of the proportions of the rare, fairly rare and less common species (i.e. respectively nrc classes 3, 4 and 5) was largest under hay-making twice a year and under hay-making in June in combination with mulching in September. Under grazing throughout the summer and under the burning management hardly any rare to less common species were found. The proportion of the rare species (nrc-3) was largest under hay-making twice a year followed by hay-making once a year in September.

Soil characteristics

Land use and management practices influence the chemical attributes in the soil, in particular the soluble plant nutrients N, P and K. Plants contain these elements so when mowings are removed these elements are removed too. In this way management can influence the fertility of the soil. In contrast to the chemical attributes, the management cannot change the physical attributes of the soil such as the clay content. Whereas soil fertilty is correlated to the clay content, on clayey soils fertility will never be as low as on sandy soils, even when the management is fully aimed at impoverishment of the soil.

Relation between management and above-ground biomass

In general, between 1988 and 1994 the peak standing crop on the experimental dike increased. In 1988 differences in peak standing crop (i.e. biomass in June) were not yet significant. In 1990 burning led to a significantly ($p<0.05$) larger PSC than grazing twice a year, hay-making twice a year, mowing in June in combination with grazing in September, hay-making once a year in September and no management. In 1992 mulching twice a year and no management led to a significantly larger PSC than hay-making twice a year.

In 1994 a peak standing crop lower than 6 ton dry weight per hectare was only found under extensive grazing throughout summer. Foraging without manuring and creating latrines leads to a reallocation of nutrients (Bakker, 1989). In this experiment the sheep were observed to visit steeper parts only to graze and to create latrines only on the less steep parts. This implies an impoverishment of the steeper parts, while less steep or level parts become enriched. However, the above-ground biomass production is not fully removed by consumption by cattle, but is also spoiled by trampling, fouling and decomposition ('t Mannetje, 1978; Lantinga, 1988). Esselink *et al.* (1989) estimated that cattle consumed 30-50% of the biomass production. Bakker (1989) found a consumption percentage of herbage utilization of 25%. This percentage would be expected to be higher in the case of grazing by sheep, since damage due to trampling is likely to be less compared to grazing by cattle. Additionally, sheep uptake biomass more efficient than cattle. Whereas sheep nibble at the vegetation, cattle take irregular bites of the vegetation.

Another factor that could lower the biomass production could be the constant trampling by the sheep. In the extensively grazed meadows the stocking rate was so high that after the grazing period all of the annual herbage increment had been utilized by the grazers. During the grazing season the stocking rate was adjusted to the biomass production; in more productive periods the stocking rate was raised whereas in less productive periods the stocking rate was lowered. Bakker (1989) found that grazing regime resulted in great differences in soil resistance, measured with a penetrometer, namely heavily grazed areas showed values of 11.5 (± 2.3) $kg.cm^{-2}$ and lightly grazed patches of 5.5 (± 0.7) $kg.cm^{-2}$. In hayfields with hardly any trampling the soil resistance will probably be lower than in grazed meadows. Another factor which may have influenced the biomass production could be the change in species composition from tall hayland species to much smaller meadow species. Besides, heavy defoliation can result in a reduction of pasture biomass (Bakker, 1989).

A peak standing crop of between 6 and 7 ton $dw.ha^{-1}$ was found under the three other grazing regimes and under hay-making twice a year. The relatively small biomass production under grazing twice a year came about for the same reasons as under grazing extensively, whereas under the combinations of grazing and hay-making the relatively small biomass production was also caused by nutrients being removed with the mowings. The relatively small biomass production under hay-making twice a year was solely attributable to the nutrient removal. A peak standing crop exceeding 8 ton dw.ha^{-1} was found under mulching twice a year and under 'no management'.

The September biomass of the management practices with cutting in June varied between 1.5 ton dw.ha^{-1} under hay-making in June in combination with grazing in September to 2.8 ton dw.ha^{-1} under hay-making twice a year. The September biomass of the management practices without cutting in June varied between 4.1 ton dw.ha^{-1} under hay-making once every two years to 6.9 ton dw.ha^{-1} under the burning regime. This could have a significant effect on seedling establishment. In 1994 annual biomass production was significantly smaller under hay-making in June in combination with grazing in September and hay-making twice a year than it was under mowing twice a year without removal of the mowings at least once.

Nutrient removal in relation to atmospheric deposition

Impoverishing of the soil can be considered as a possible cause of floristic change and increase of species richness. Whether and how rapidly a soil can be impoverished depends on the soil characteristics, the nutrient removal by the management regime applied, which is related to the nutrient pool in the soil and the atmospheric deposition of the main plant nutrients. In the Netherlands, the mean atmospheric deposition of inorganic nitrogen is estimated between to be 40 and 50 kg N ha^{-1} yr^{-1} (Fransen, 1987; Schneider & Bresser, 1988; Bobbink *et al.*, 1990). On clayey soils only about 5 kg N.ha^{-1} is washed out yearly (Van Dam, 1990). So nitrogen impoverishment by management only takes place when more than 35 to 45 kg N.ha^{-1} is removed by hay-making practices. Assuming a nitrogen content of 1.27% in the total above-ground biomass, more than 2.8 to 3.5 tons dry matter should be removed per ha every year.

Assuming an atmospheric deposition of 50 kg N ha^{-1}.yr^{-1}, nitrogen is actually decreased under hay-making twice a year, hay-making in June in combination with mulching in September, hay-making once a year in June and hay-making in June in combination with grazing in September. Under hay-making once a year in September the amount of nitrogen removed is equal to the nitrogen input by atmospheric deposition. Mulching twice a year and hay-making once every two years lead to nitrogen accumulation. Grazing in flat meadows hardly removes any nitrogen (Bakker, 1989). A grazing animal returns more than 90% of the nutrients it consumes, as dung and urine (Wilkinson & Lowry, 1973; Perkins, 1978). The nutrients in urine are immediately available to plants, those in dung less, but the decay rate of faeces is considerably higher than standing dead or litter material (Perkins *et al.*, 1978). A net loss of nutrients can only be expected from wool, meat and carcasses and by volatilization of nitrogen. These losses amount ony a few kg ha^{-1}.yr^{-1} and are often more than compensated by the input from rainfall (Green, 1972; Perkins, 1978; Bülow-Olsen, 1980). In these circumstances, grazing on clayey soils will always lead to nitrogen accumulation. Furthermore, grazing stimulates the decomposition of organic material (Breymeyer, 1978; Perkins *et al.*, 1978), and hence mineral cycling of N, P, Ca, Mg, Mn and P (Floate, 1970; Spedding, 1971, Bülow-Olsen, 1980). However, in meadows with steep slopes foraging without manuring and creating latrines leads to a reallocation of nutrients (Bakker, 1989). In the present experiment the sheep were observed to visit steeper parts only to graze and to create latrines only in the less steep parts. Foraging without manuring and creating latrines leads to a reallocation of nutrients. This implies an impovershment of the steeper parts, while in the less steep or level parts nutrients accumulate. Because of the fact that under hay-making once a year in September the nitrogen removal approximately equals the nitrogen input by atmospheric deposition, grazing in June in combination with hay-making in September will probably result in a small net nitrogen removal. Since nitrogen appeared to be limiting the production, a net nitrogen removal will probably cause the above-ground biomass to decrease, thereby bringing about a further increase of the species diversity. The deposition of P is estimated between 0.3 and 1.7 kg ha^{-1}.yr^{-1} with a mean value of 1 kg ha^{-1}. yr^{-1}. With the exception of mulching twice a year, under all management practices the amount of phosphorus removed exceeded the phosphorus input by atmospheric deposition. The deposition of K is estimated between 10 and 20 kg ha^{-1}.yr^{-1} with a mean value of 15 kg ha^{-1}.yr^{-1} (Katznelson, 1977; Marrs *et al.*, 1983; Heij & Schneider, 1991). Assuming 15 kg K ha^{-1} .yr^{-1}, potassium was actually removed by all hay-making practices applied and also by hay-making in

June in combination with grazing in September and probably also by grazing in June in combination with hay-making in September. Under mulching, under the grazing regimes and under the burning management potassium probably accumulates. Since nitrogen appeared to be limiting the production, a net phosphorus or potassium removal will have only little effect on species diversity. In the future, however, potassium may limit biomass production.

The mowings must be removed as soon as possible after mowing. The longer they remain in the field, the greater is the leakage of nutrients out of the biomass (Schaffers, 1995; Schaffers *et al.*, 1998). Removing the mowings one week after mowing means a loss in removed biomass of 1 (to 2.4) ton $dw.ha^{-1}.yr^{-1}$. Removing the mowings after 4 weeks after mowing means a loss of 2.2 to 5 tons $dw.ha^{-1}.yr^{-1}$, 25 to 100 kg $N.ha^{-1}.yr^{-1}$, 2 to 10 kg $P.ha^{-1}.yr^{-1}$ and 40 to 200 kg $K.ha^{-1}.yr^{-1}$. Thus, the hay fields should be mown in good weather so the mowings dry fast and can be collected within two or three days.

The conclusions presented in the literature about the impovershment of the soil vary. In contrast with some authors who found a decrease in N, P and K after years of hay-making in order to impoverish the soil (Wind, 1980; Elberse *et al.*, 1983, Oomes & Mooi, 1985), others found increases in one or more macro nutrients (Schiefer, 1983; Bakker, 1989). Miles (1985, 1987) stressed that plants not only depend on soil chemical factors, but do themselves induce changes in the soil, which results in complex interrelationships. Petel (1987) reviewed examples of the dynamic character of the soil system and the changes in availability of nutrients as a result of release by weathering of parent materials, dissolution of poorly soluble compounds, decay of organic matter in the soil and absorption by plant roots. In many studies changes in pH were found. Bakker (1989) found a decrease of pH (KCl) in all the hay-making regimes. Miles (1987) points to the considerable effects of changing pH on other soil parameters. The decrease in pH often results in a higher solubility of ions, particularly from the iron compounds; for example, occluded phosphate (Kinzel, 1982).

In a comparison of grazing and hay-making Bakker (1989) found a much higher poor to rich species ratio in the lightly grazed area and a slightly higher ratio in the heavily grazed area than in the hay-making regime in the Westerholt study area. A higher poor to rich species ratio means a larger proportion of species indicating poor soil conditions. In the same study area Bakker found no difference in soil chemical composition between grazing and hay-making and no decrease of macro nutrients. In the Loefvledder study area Bakker (1989) found that the amount of nitrogen removed in hay was similar in 1975 and 1983, but less phosphorus and potassium were removed in 1983 than in 1975. P and K combined or singly seem to be limiting in this area.

Nutrient removal is not constant throughout the season. Hay-making in May removes smaller amounts of nutrients than later cuts (Schmidt, 1981; Dickinson & Polwart, 1982; Buytendorp *et al.*, 1983). Additionally, a smaller amount of nutrient removal has been found in late autumn than in the summer (Kapfer & Pfadenhauer, 1986; Egloff, 1986). In a comparative study of nitrogen flows of two meadow ecosystems Berendse *et al.* (1994) concluded that the nitrogen balances showed that the inputs through atmospheric deposition and the outputs through hay removal are quantitatively the most important components of the nitrogen balance. Nevertheless, the nutrient removal related to the nutrient pool in the topsoil only accounts for a small percentage (Bakker, 1989). Dickinson (1984) estimated that less than 1% of the total eco-system nutrients were removed per year as cuttings. It can be concluded that nutrient depletion, if any, is apparently a very slow process.

Impact of management on nitrogen mineralization

The size and activity of the active N pool must be known to be able to predict soil N availability for plants over the growing season, but this knowledge is in itself insufficient. The flux of N is the product of the N pool size and and its specific mineralization rate constants (Rutherford & Juma, 1989). Consequently, a soil with a low organic-N content, but a high specific mineralization rate, may mineralize as much N as a soil with a high organic-N content and a low specific mineralization rate. Therefore, comparison of pool sizes between soils does not provide enough variation to understand N dynamics. It is for this reason that the availability of nitrogen to plants was determined by measuring the internal recycling within the soil system. An extremely high mineralization was measured under burning and a relatively low mineralization under grazing twice a year, no management and mowing in June in combination with grazing in September. In all management practices N-mineralization in period I (28 March - 9 May) was higher than in period II (9 May - 20 June). In period I the mean N-mineralization over all management practices was 412 g $day^{-1}.ha^{-1}.dm^{-1}$ and in period II it was 265 g $day^{-1}.ha^{-1}.dm^{-1}$. Schaffers (1995) also found highest mineralization rates between March and June in *Arrhenatheretum* hayfields in road verges, in particular for the *Arrhenatheretum picriditosum*. He measured maximum mineralization rates for this vegetation of between 400-600 g $day^{-1}.ha^{-1}.dm^{-1}$. For dry, neutral to basic grasslands he estimated a peak in mineralization of 400 g $day^{-1}.ha^{-1}.dm^{-1}$. This peak is reached between mid-April and the end of May. Since the mineralization strongly depends on moisture and temperature, the time that the peak of mineralization is reached probably differs each year (Schaffers, 1995).

The mean momentaneous NO_3, NH_4 and $N_{mineral}$ contents of the soil clearly decreased between 28 March and 20 June. This decrease is probably caused by the uptake by plants. Nevertheless, in the present study no correlation was found between the decrease of momentaneous N and the above-ground biomass production. The mineralization rate is likely to be a good measure of nutrient availability in fen communities (Vermeer & Berendse, 1983) and has been positively correlated to the above-ground production in heathland communities (Berendse, 1986). However, it is difficult to measure and is probably affected by many factors such as the weather and the hydrological conditions. In addition, the vegetation influences soil properties and hence soil productivity. In the course of a few years changing patterns of vegetation will trigger changed patterns of labile soil properties such as pH (Miles, 1985, 1987). The soil pH largely controls the C/N ratio of litter and humus and thereby the rate of their decomposition and the rate of nitrogen mineralization.

Relation between management and vegetation pattern

Differences in grazing intensity are particularly interesting for nature conservation if they result in patterns in the structure of the sward. Such patterns of closely grazed areas and lightly grazed patches should remain constant for several seasons and years, as otherwise different plant communities adapted to these environmental circumstances will be unable to emerge. Bakker (1989) concluded that the micro-patterns he found did not change randomly from year to year, but were dependent on the grazing regime. He found that the species composition in heavily grazed areas differed from lightly grazed patches. The presence of species differed only slightly, but their biomass differed considerably. Repeated defoliation in heavily grazed areas stimulates tillering (Harper, 1977; Witchi & Michalk, 1979). More young leaves and a higher leaf:stem ratio increase preference (Davies, 1925), probably due to a higher percentage of crude protein and a greater digestibility of forage (Stobbs, 1973). Thus, heavily grazed areas have a higher forage quality than the lightly grazed patches (Bakker, 1989). Since there is a preference for specific sites with a high forage quality, the sheep maintain these sites, including different species, by their feeding strategy (McNaughton, 1979; Drent & Prins, 1987, Wallis de Vries & Daleboudt, 1994). The grazing regime resulted in great differences in soil resistance, measured with a penetrometer; heavily grazed areas had values of 11.5 (± 2.3) $kg.cm^{-2}$ and lightly grazed patches of 5.5 (± 0.7) $kg.cm^{-2}$.

In the present study there seemed to be two ways of creating vegetation patterns under the grazing practices. First, the sheep enlarged the foraging area by exceeding the boundary of the initial foraging area which initially consisted of only the level or almost flat lower parts of the dike. Additionally, their foraging on the steeper parts of the slope was more selective than it was on the more level parts. On the steeper slopes a mosaic of taller clumps interspersed with shorter turf emerged. The diameter of the taller clumps ranged from 0.20 m to several metres. This mosaic is referred to as a micro-pattern. The heavily grazed areas had a canopy height less than 5 cm and hardly any litter accumulation, the lightly grazed patches had a canopy height of more than 10 cm and more litter accumulation. The micro-pattern was first observed three years after the reconstruction of the experimental river dike. Only then was a clear difference between heavily and lightly grazed areas recognizable. The micro-pattern was clearest under grazing throughout the summer, with grazing twice a year in second place, followed by grazing in spring and mowing in autumn. Hay-making in June in combination with grazing in autumn showed hardly any micro-pattern. Grazing in the early growing season seems to have had a particular impact in creating a micro-pattern. This is because at that time there is plenty of food, so sheep can be more selective. Milner & Gwynne (1974) suggested that selection by the sheep for species palatability is only possible during the late spring and early summer when there is a considerable choice. During the rest of the year selection is limited by availability .

Under all grazing practices with grazing in September, sheep remained in the meadows until they had used up all the annual herbage increment. After this grazing period hardly any structure patterns were discernable, whereas in the following summer the pattern could again be recognized, largely because of the different grass species compositions.

Vegetation pattern is also influenced by the mowing frequency. The species richness showed greater differences between the smaller plots (0.25 m^2, 1 m^2 and 4 m^2) than between the total permanent plots (24 m^2). Parr & Way (1988) also found that increased cutting frequency significantly decreased the frequency of several mainly coarse-growing species, including *Elymus repens*, *Arrhenatherum elatius*, *Alopecurus pratensis*, *Cirsium arvense* and *Anthriscus sylvestris*. In contrast, many finer species (mostly grasses) increased in frequency. They concluded that species richness per plot of 225 cm^2 was affected more by changes in cutting frequency than species richness per plot of 1.8 x 18.3 m. In other words, even if species richness of total plots is the same, species richness within the plots can differ to a certain extent. The more frequent the mowing, the finer the vegetation pattern is.

Relation between management and canopy structure

The ability of species to spread or to invade is expected to be affected by the structure of the sward. Germination and seedling establishment is influenced by a variety of environmental factors (e.g. Silvertown, 1980, 1981; Fenner, 1987; Masuda & Washitani, 1990). The canopy structure of the vegetation, which determines both light penetration to the soil surface and microclimate, seems to be an important determinant of the onset of germination and seedling establishment (Oomes & Elberse, 1976; Verkaar *et al.*, 1983; Fenner, 1985; Goldberg, 1987). Not only the above-ground phytomass of a stand but also its canopy structure is important for the species diversity (Wheeler & Giller, 1982; Fliervoet, 1984; Bakker, 1989). An erect growth form allows much light to reach the soil.

In the present study differences in biomass were particularly caused by differences in biomass above 30 cm height. At 'no management' a relatively high biomass was measured in the layer 70 tot 100 cm height and above 100 cm height. At mulching twice a year, mowing once every two years and grazing in combination with hay-making in September a relatively high biomass was measured in the layer 70 to 100 cm height. Comparison of two sections with different clay content showed that at the higher clay content (section C: clay content 36.4%) the biomass in all height layers was somewhat higher than at the lower clay content (section D: clay content 21.6%) which caused a higher overall biomass on the higher clay content.

Relation between canopy structure and species richness

Two levels of vegetation patterns can be distinguished (Wallis de Vries & Schippers, 1994): (a) micro-pattern (fine-scale; vegetation units can be considered separately) and (b) macro-pattern (coarse-scale; vegetation units are combined and differentiate at landscape level). In the present study in the pastures only micro-patterns were observed, due to the relatively short period of study and the relatively high grazing densities. Generally, macro-patterns are only found in pastures with a large surface area and low grazing intensities. Because of the equal management intensity all over the haylands they hardly showed any micro-pattern.

Bakker (1989) found that, although seedlings emerged in all management regimes, the emergence and survival to juvenile and flowering individuals was highest in the plots with the twice a year hay-making regime and the hay-making in September regime and lowest in the uncut plots. In the present study the highest species diversity was also found at hay-making twice a year followed by hay-making once a year in September. When only comparing mowing practices and no management, the latter showed to lead to the lowest species diversity, in conformity to Bakker (1989).

Grazing intensity also influences the emergence and the fate of the seedlings. In particular rosette plant species such as *Hypochaeris radicata*, *Taraxacum sp.*, *Leontodon autumnalis*, *Bellis perennis* and *Plantago major* establish better in heavily grazed areas than in lightly grazed pastures. Furthermore, these species have a higher frequency percentage in a grazed area than in a hayfield (Elberse *et al.*, 1983). Therefore, it can be assumed that the short turf in the heavily grazed sward provides more safe sites for these rosette plants than the hay-making regime with its taller canopy. Species with a more erect growth form will be favoured by a hay-making regime. In the present study the species diversity of haylands was higher than of meadows grazed by sheep only and meadows grazed in June in combination with hay-making in September. Concerning grazing management only hay-making in June in combination with grazing in the autumn appeared to lead to a relatively high species richness.

Relation between management and light penetration

In this section the light penetration is used to quantify the structure of the sward in June. The light penetration to the soil surface seems to be an important determinant of the onset of germination and seedling establishment. This light penetration is especially determined by the canopy structure of the vegetation (Oomes & Elberse, 1976; Verkaar *et al.*, 1983; Fliervoet, 1984; Fenner, 1985; Goldberg, 1987). In general the canopy density increases during the spring and early summer and reaches its maximal value in June (Campino Johnson, 1978; Fliervoet, 1984; Bakker, 1989). In the present study the structure or the density of the canopy, expressed as the light penetration to the soil surface, differed considerably between the management practices. In June the canopy density was lowest under hay-making twice a year. This is in agreement with the results of Bakker (1989) who found a higher vertical view through the vegetation in the September and in the both in July and September hay-making regimes than in the other regimes. The canopy density was highest under the burning regime, under hay-making once every two years and under the grazing twice a year regime.

Relation between light penetration and species richness

The emergence and survival of seedlings is positively correlated to the percentages of full sunlight reaching the soil surface (Mølgaard, 1977; Goldberg & Werner, 1983; Schenkeveld & Verkaar, 1984). The leaf canopy not only changes the quantity of light but also changes its quality at soil level. The lower red:far red ratio under a plant canopy can reduce the emergence and seedling establishment of various species (Silvertown, 1980). In the present study only positive correlations were found between the species richness and the far-red, green and total light. No positive correlation was found between the species richness and the ratio red:far-red. Numerous alternative explanations for the effects of productivity on diversity have been proposed. Grime (1973, 1979), for instance, suggested that productive habitats have lower diversity because of more intense competition. Newman (1973) countered that competition is equally strong in both fertile and infertile habitats, but that in productive habitats strong competition for light inherently favours the tallest species, whereas in infertile habitats many alternative traits confer competitive ability for nutrients and thus allow numerous species to coexist. Goldberg & Miller (1990) suggested that the decrease in light penetration caused by increased productivity should increase mortality rates for slow-growing or shade-intolerant species and for seedlings, and thus increase local extinction rates. Tilman (1993) also found that species richness was significantly higher in plots with higher light penetration through the vegetation but he emphasized that diversity in productive grasslands is lower because of accumulated litter. According to Fliervoet (1984) in grasslands with a clear stratification of biomass the proportion of bryophytes and lichens appears to be dependent on the amount of incident light reaching the moss layer. So canopy structure also appears to effect the moss layer in grasslands.

5.5 CONCLUSIONS

The clay content of the soil of the experimental dikes appeared to be positively correlated to the electrical conductivity, the organic matter content, the total nitrogen content, the potassium content and the C/N quotient, and negatively with the sand content, the acidity, the lime content and the calcium content. Van der Zee (1992) described nine plant communities on river dikes in the whole fluviatile district. On the basis of the clay contents the occurrence of one of these nine communities, the *Medicagini-Avenetum centaureetosum scabiosae*, is not possible on the experimental river dike, whereas the variant with *Galium verum* and *Pimpinella saxifraga* and the variant with *Galium verum* and *Agrostis capillaris*, both variants of the *Arrhenatheretum* sub-association group B *brizetosum*, are less likely to occur. The other six communities can possibly occur.

In 1994 the total number of species and the number of herb species were inversely correlated with the above-ground biomass in June. The number of species appeared to be positively correlated with the amount of penetration of far-red and total light.

Methods of reconstruction

Each method of recontruction appeared to have distinctive soil characteristics. In the spared zone the clay content was relatively low and the sand content relatively high. The complete sods differed most from the other methods of reconstruction. Their clay content was relatively high and the sand content relatively low. Their soil fertility, nitrogen mineralization and CN-ratio were highest of all methods of reconstuction. Consequently, in 1994 the largest biomass in June was measured on the replaced complete sods whereas the smallest biomass was measured on the replaced topsoil. In 1994 the species richness was highest in the spared zone and lowest on complete sods. In 1994 the proportion of rare to fairly common species was highest in the spared zone, followed by the imported clay and replaced topsoil, and lowest in the complete sods.

Differences in species richness between the different methods of reconstruction were already apparent in the smallest area determined (i.e. 0.25 m^2). The species richness in 1 m^2 in the spared zone and on replaced topsoil was already higher than it was in 24 m^2 in the other methods of reconstruction. Whereas the species richness in 24 m^2 was almost equal on replaced sods, replaced subsoil and imported clay, in 0.25, 1 and 4 m^2 it was significantly lower on imported clay.

Sowing

Whereas in the first years after the reconstruction the method of reconstruction and the sowing were the most important factors, in 1992 and 1994 the management became more important. In 1994 there were no longer any significant differences in species diversity between the different sowings.

Whereas sowing seeds gathered locally appeared to accelerate the development of the vegetation, the development of the unsown permanent plots was somewhat slower but by 1994 they had reached the same stage. Addition of *Lolium multiflorum* did not seem to affect the development, sowing with BG5 appears to retard the vegetation development.

Management

In 1994 a peak standing crop of less than 6 ton dry weight per hectare was only found under grazing throughout the summer. A peak standing crop between 6 and 7 ton $dw.ha^{-1}$ was found under the three other grazing regimes and under mowing twice a year with removal of the hay. A peak standing crop exceeding 8 ton $dw.ha^{-1}$ was found under mowing twice a year without removal of the hay and under 'no management'. The amount of penetration of far-red and total light was highest under hay-making twice a year and low under burning, hay-making once every two years and grazing twice a year.

Nitrogen was actually removed under hay-making twice a year, hay-making in June in combination with mulching in September, hay-making once a year in June and hay-making in June in combination with grazing in September. Under hay-making once a year in September the amount of nitrogen removed was equal to the nitrogen input by atmospheric deposition. Mulching twice a year and hay-making once every two years led to nitrogen accumulation. Grazing results in hardly any nitrogen being removed and therefore, on clayey soils, grazing practices always lead to nitrogen accumulation. With the exception of mulching twice a year, under all management practices the amount of phosphorus removed exceeded the phosphorus input by atmospheric deposition. Potassium was actually removed by all mowing regimes except mulching twice a year.

In 1994 the species richness under hay-making twice a year was significantly higher than under hay-making once every two years, mulching twice a year, grazing twice a year, no management, grazing in June in combination with hay-making in September, grazing throughout the summer and burning. When comparing the four most frequent mowing managements, the significantly highest number of species had already appeared in the smallest determined surface area of 0.25 m^2. The species richness under hay-making twice a year was already higher in 4 m^2 than it was in 24 m^2 under the other management regimes.

In 1994 the proportion of rare to less common species was highest under hay-making twice a year and under hay-making in June in combination with mulching in September. Under grazing throughout the summer and burning hardly any rare to less common species were found.

Plant communities

The mean clay content of the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) was significantly lower compared with the other communities. On the other hand, the mean clay content of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III), the second best developed plant community after the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I), was the highest. Within the range of clay contents on the experimental river dike, the development of species-rich grassland vegetation is possible even on the heaviest clay, but only under optimal management practices.

In 1994 the peak standing crops of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) and of the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) were significantly smaller compared with the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) and the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). The biomass of the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) was significantly larger than that of communities III and IV. Penetration of far-red and total light was relatively high in the best developed plant community *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) and the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) and a relatively low light penetration in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II).

Appendix 1. Soil characteristics of the plant communities.

Table 71. Mean EC, organic matter-%, Ntot, Ptot, CN, NP, K and Ca per plant community. Homogeneous groups at p<0.05 level.

Plant comm.	EC	Homogeneous groups	Plant comm.	Organ. mat-%	Homogeneous groups
II	240	a .	VII	2.12	a . .
III	239	a .	I	1.89	a . .
IV	231	a b	II	1.73	a b .
V	223	. b	III	1.56	. b c
I	217	. b	VI	1.53	. . c
VI	215	. b	V	1.48	. . c
VII	215	. b	IV	1.43	. . c

Plant comm.	Ntot mg/kg	Homogeneous groups	Plant comm.	Ptot mg/kg	Homogeneous groups
VII	2206	a .	VII	504	a
II	1755	a .	II	496	a
III	1697	a b	V	487	a
I	1641	. b	VI	484	a
VI	1510	. b	III	483	a
V	1489	. b	I	475	a
IV	1255	. b	IV	471	a

Plant comm.	C/N	Homogeneous groups	Plant comm.	N/P	Homogeneous groups
I	11.5	a .	VII	4.38	a . . .
IV	11.5	a .	II	3.52	. b . .
V	11.1	a .	III	3.50	. b . .
VI	10.5	a b	I	3.45	. b c .
II	10.1	a b	VI	3.11	. . c d
VII	9.6	. b	V	2.98	. . . d
III	9.3	. b	IV	2.71	. . . d

Plant comm.	K mg/kg	Homogeneous groups	Plant comm.	Ca mg/kg	Homogeneous groups
III	9566	a .	I	20612	a . .
II	9470	a .	IV	18928	a b .
VII	9455	a .	III	15977	. b .
IV	8752	a b	II	15677	. b c
VI	8444	. b	V	14193	. b c
V	8286	. b	VI	14012	. b c
I	7824	. b	VII	10716	. . c

Appendix 2. Plant communities on river dikes, described by Van der Zee (1992) and possibility of developing on the experimental river dike (+ = possible, +/- = less likely, - = not possible).

Comm. 1	*Medicagini-Avenetum centaureetosum scabiosae*	-
Comm. 2	*Arrhenatheretum* sub-ass. B: *brizetosum*, variant with *Galium verum* and *Pimpinella saxifraga*	+/-
Comm. 3	*Arrhenatheretum* sub-ass. B: *brizetosum*, variant with *Galium verum* and *Agrostis capillaris*	+/-
Comm. 9	*Arrhenatheretum*, transition community with *Origanum vulgare* and *Euphorbia esula* [subass. A / subass. B]	+
Comm. 12	*Arrhenatheretum* sub-ass. A: variant with *Potentilla reptans* and *Galium mollugo*	+
Comm. 14	Fragmentary community with *Alopecurus pratensis* and *Heracleum sphondylium* [*Arrhenatherion / Artemisietea*]	+
Comm. 17	*Lolio-Cynosuretum*, sub-ass. group B, *ononidetosum*	+
Comm. 21	*Poo-Lolietum*	+
Comm. 22	*Lolio-Plantaginetum*	+

CHAPTER 6

EFFECT OF VEGETATION COMPOSITION AND MANAGEMENT ON THE EROSION RESISTANCE OF RIVER DIKES

6.1 INTRODUCTION

A well closed vegetation is an important protection against soil erosion. Soil factors such as bulk density, plasticity, clay content, sand content, cohesion, permeability, organic matter content, salt concentration, cation content, lime content and type of clay mineral also influence resistance to erosion.

On a slope covered with a grass sward even a firm stream of water causes only little erosion because the energy of the flowing water is reduced by friction with the tough and elastic blades of grass. Even if the above-ground parts of the plants are washed away, intermeshing root systems remaining in the upper soil still show a very great resistance to erosion (Waterloopkundig Laboratorium & Laboratorium voor Grondmechanica, 1984). Without vegetation the force of erosion acts directly on the bare soil surface and soil particles are removed more easily. The erosion on bare soil is usually many times greater than on a soil covered by vegetation (Strahler, 1969; Morgan, 1979; Batie, 1983; Overkamp, 1985). The denser and deeper the root growth of a vegetation, the more the damage and possible destruction caused by erosion will be delayed (Thierry *et al.*, 1958).

Thus, for maximum protection of the dikes the vegetation canopy should be closed and resistant to erosion, especially in the season with the greatest probability of high water. The swards on both slopes of the dike must meet these conditions. This chapter describes the research on the development of the civil engineering quality of the plant communities on the experimental dike and the influence of the method of reconstruction, sowing and management on erosion resistance. The following four attributes representing the civil engineering quality of the sward were investigated: 1) the openness of the sward, 2) the ground cover, 3) the root density and distribution and 4) shear resistance.

6.2 METHODS

For a description of the location of the experimental site and the experimental set-up, see chapter 2. For a description of the plant communities see § 3.3.1. For a description of the management practices see § 2.2.

Two attributes which represent the civil engineering quality of the sward surface are 1) the openness of the sward, expressed as the mean surface of the bare areas and in the distribution of the bare areas over size categories and 2) the ground cover, expressed as the percentage of the soil surface covered by vegetation. Attributes which represent the civil engineering quality of the underground part of the sward are root density and root distribution. The relative civil engineering quality of the sward can be defined in terms of the shear resistance of the soil-root complex.

The sward openness, the ground cover, the root density and distribution and the shear resistance were measured in the period mid-March to mid-April in 1989, 1990, 1993 and 1994. In this period the probability of the occurrence of high water is greatest and the condition of the vegetation is worst and it is often damaged by frost.

6.2.1 Openness of the sward

The openness of the sward in the permanent plots was measured by means of a ring experiment (Neuteboom, 1991). Within each permanent plot the openness was sampled at 100 points. Using concentric rings with increasing diameters (see figure 36 and table 72) the distance between a pin randomly stuck into the soil and the nearest rooted shoot was determined. The mean size of the bare areas in the permanent plot was then calculated.

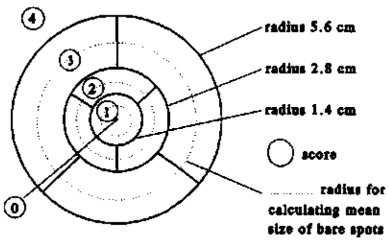


Figure 36. Schematic presentation of the set of rings.

Table 72. Radius, mean radius and mean area of the separate rings.

	Radius (cm)	Mean radius (cm)*	Mean area (cm^2)**
pin	0.125	0.0625	0.01
1^e ring	1.4	0.7625	1.83
2^e ring	2.8	2.1	13.85
3^e ring	5.6	4.2	55.42
4^e ring	11.2	8.4	221.67
5^e ring	16.0	13.6	581.07

* radius of imaginary circle in the middle of the rings
** area on the basis of the mean radius

Mean size of the bare areas
The openness, expressed in the mean size of the bare areas in the sward, was calculated with the following equation:

$$H = (a*0.01+b*1.83+c*13.85+d*55.42+e*221.67+f*581.07)/100 \text{ cm}^2$$

in which a = number of times the pin touched a shoot; b = number of times the pin did not touch a shoot but a shoot was found within the first ring, c = number of times a shoot was found within the second ring, etc.; $(a+b+c+d+e+f=100$ at 100 cuts per permanent plot). In 1989 the openness of the sward was measured in 64 permanent plots, in 1990 in 37, in 1993 in 102 and in 1994 in 94 plots. The openness of the sward was determined for the plant communities and the management practices in all years of research.

Size distribution of the bare areas
Although a permanent plot with only a few large bare spots can have the same degree of openness as one with many small bare spots, its civil engineering properties are far worse. The roots of adjacent plants venture into the soil under small bare areas and provide some cohesion, but the centres of large bare spots are not stabilized in this way. To investigate this, the mean size of the bare spots and their size distribution were determined. The size categories used were the areas within the concentric rings (see table 72). The size distribution of the bare areas was determined for the five main plant communities and the management practices in 1994.

6.2.2 Ground cover

The ground cover (i.e. vegetation cover) in the permanent plots was defined using a metal frame with cross-wires of string interwoven and pulled taut, giving 11 x 11 subdivisions and 100 points of intersection. This frame was laid down randomly four times per permanent plot and each time a needle was let down at the 100 intersections. It was noted whether the needle touched bare ground or vegetation. Before measuring, the vegetation was clipped to 2 cm above the ground and all the cut material was removed. In all, 4 x 100 = 400 intersections were pricked in each permanent plot. The ground cover was calculated using the equation:

Ground cover % = (*V*/400) * 100%

in which *V* is the total number of measurements in which vegetation was encountered. In 1989 the ground cover was measured in 47 permanent plots, in 1990 in 37, in 1993 in 69 and in 1994 in 127 permanent plots. The ground cover was determined for the plant communities and the management practices in all years of research.

6.2.3 Root research

The roots of terrestrial plants are involved in the acquisition of water and nutrient, anchorage of the plant, synthesis of plant hormones, and storage functions (Schiefelbein & Benfey, 1991). The development of a root system involves strategies that are common to the development of all plant organs, as well as certain aspects that are unique to roots. Despite the importance of roots and some unusual developmental characteristics, the study of root morphogenesis has not received as much attention as the development of aerial plant organs.

When describing a root profile the root density per unit of volume and the root distribution in the root profile (i.e. root density per unit of depth) are important. The root density can be expressed in root length and root weight per unit of volume. In terms of erosion resistance the total length of roots per unit volume of soil is the most appropriate way to characterize the root density. However, it is very laborious to determine total root length. It is simpler and quicker to weigh roots. Therefore in many cases only the total root weight per unit volume was taken when determining the root density. However, the disadvantage of using root weight as a measure of the root density when examining the relation between root density and erosion resistance is that large, inactive main roots make up the bulk of the total root weight. The root length is preferable to the root weight as a measure of the density of the root system in the soil. Therefore it is advisable to determine the total root length per unit volume of soil as well as the root weight and moreover to calculate the root length/root weight ratio.

Sampling and analysis

Root samples were obtained from 45 permanent plots in early April 1994 using an auger with a diameter of 8.5 cm, designed for sampling roots. Each 10 cm was sampled separately up to a depth of 50 cm. Samples were not taken deeper than this because previous research had shown that the total amount of roots at a depth between 50 and 100 cm is only a few per cent of the total root material found between 0 and 50 cm (Sýkora & Liebrand, 1987). The first 10 cm sample was divided into three sub-samples: 0-3 cm, 3-6 cm and 6-10 cm. The second 10 cm sample was divided into two sub-samples: 10-15 cm and 15-20 cm. Subsequently, each sample of 0 to 50 cm depth consisted of 8 sub-samples. Each sampling was carried out in triplicate per permanent plot. The sub-samples were packed in polythene bags and stored at -25 °C until analysed. For the analysis the sub-samples were washed and the root material was separated from the soil material using sieves of various gauges. The root length per layer was ascertained using a transparent, plastic counting tray. The bottom of this tray is sub-divided by 21 horizontal and 14 vertical lines giving 22 x 15 subdivisions. After spreading the roots in a shallow layer of water as evenly as possible, the number of times the roots intersected the lines in the counting tray were determined. If this number was too large to count, it was estimated. The total length of the roots in a sub-sample was then calculated using the following equation:

$$R = \frac{\pi . n . O}{2 . L}$$

in which R = total length of the roots (m), n = number of intersections between roots and lines, O = area on which the roots lie in counting tray (m^2) and L = total length of the lines counted along (m). The root density (in root length) is R/volume soil ($m.dm^{-3}$). After the total amount of roots in each sub-sample had been counted, the dry weight was determined. The root density (in root weight) is dry weight/volume ($g.dm^{-3}$). Subsequently, the root distribution over the soil profile was calculated. The root distribution was expressed in absolute amounts as well as in proportions. The root length and root weight were determined for the five main plant communities and the management practices in 1994.

Relation between root length and root weight: specific root length
The relation between the root length and the root weight was determined from 240 root samples . The linear regression coefficient between root length and root weight is 0.846 (r^2=72%). The linear regression coefficient between root length and the square root of the root weight is 0.853 (r^2=73%). The regression equation is:

$$LENGTH = 79.33 * \sqrt{WEIGHT}$$

Root length is in metres, root weight in grams.

6.2.4 Shear resistance

The shear resistance of the sward indicates the force which must be exerted before the sward shears. This resistance is defined by many factors. One of them is the adhesion between soil particles and plant roots (van der Zee, 1992). Shear resistance is measured with a shear vane (i.e. field inspection vane tester) consisting of three parts (see figure 37): the upper part (no. 2) with the handle (no. 1), the graduated ring (no. 3) and the lower part (no. 4) that ends in the paddles (the 'vane'; no. 5) (see figure 37). The paddles are inserted into the soil to the desired depth. By turning the handle clockwise, force is exerted on the paddles. As long as this force is less than the resistance in the sward (root-soil complex), the paddles will not rotate, but the graduated ring does rotate. When the force exerted by the paddles exceeds the resistance in the sward, the sward shears and the paddles rotate too, together with the graduated ring. This enables the maximum force below which the paddles do not rotate to be read. This is the maximum shear resistance of the sward.

The shear resistance was measured at two depths in the soil: 0-4 cm and 10-14 cm. A correction was subsequently applied to the deeper measurement to remove the resistance caused by the bar above the paddles. Each of the four paddles is 10 x 40 mm. The resistance is read in kiloPascal (1kPa = 0.1 $N.cm^{-2}$). Twenty measurements were performed in 127 permanent plots in early

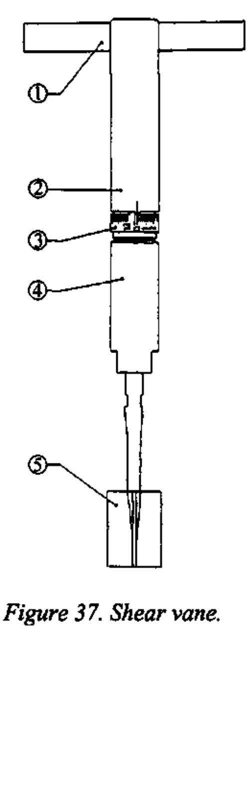


Figure 37. Shear vane.

April 1994. Subsequently, the mean shear resistance per permanent plot was determined separately for both depths. The measurements were performed in the same period in which the openness of the sward and the root density were determined in 1994. The shear resistance was determined for the five main plant communities and the management practices in 1994.

6.2.5 Classification into quality categories

On the basis of the results of a study done on the IJsselmeer dikes (Liebrand, 1993) together with the results of this research, quality classes were distinguished for all attributes important for the erosion resistance of the sward.

Openness of the vegetation
Quality classes were distinguished for the openness of the vegetation (see table 73). The openness of the vegetation is expressed as the mean surface of the bare areas (in cm^2) occurring in the vegetation.

Table 73. Classes for estimating sward openness.

Quality class	Limits (cm^2)	Valuation
1	0 - 1	excellent
2	1 - 2.5	very good
3	2.5 - 5	good
4	5 - 7.5	moderate
5	7.5 - 10	poor
6	> 10	very poor

Table 74. Quality classes for the ground cover.

Quality class	Limits	Valuation
1	> 90 %	excellent
2	75 - 90 %	very good
3	60 - 75 %	good
4	45 - 60 %	moderate
5	30 - 45 %	poor
6	< 30 %	very poor

Ground cover
In the report 'Erosion resistance of grass on clayey slopes' (Waterloopkundig Laboratorium & Laboratorium voor Grond mecha nica, 1984) it is assumed that acceptable coverage starts with 75% ground cover, increasing to 90% for a very closed state. The 6 classes in ground cover distinguished by Van der Zee (1992) were slightly modified in the light of the results of a study on IJsselmeer dikes (Liebrand, 1993) and the data from the present research (see table 74).

Root density and root distribution
Quality classes were distinguished for the root density using the considerations mentioned above. Both the root length and the root weight were divided into 6 classes (see table 75).

Table 75. Qualification of the root density on the basis of root length and root weight.

Quality class	Root length ($m.5dm^{-3}$)	Valuation	Root weight ($g.5dm^{-3}$)
1	> 1200	excellent	> 16
2	900 - 1200	very good	14 - 16
3	750 - 900	good	12 - 14
4	600 - 750	moderate	10 - 12
5	450 - 600	poor	8 - 10
6	< 450	very poor	< 8

In accordance with Van der Zee (1992), three categories of root systems were distinguished to assess the root distribution: 'deep', 'normal' and 'shallow'. Table 76 shows the boun daries between these categories for the root length. For example, a root system is deep when less than 50% of the total root length (less than 65% of the total root weight) is found in the layer up to 10 cm below ground level and more than 17% of the total root length (more than 14% of the total root weight) is found in the layer 30 to 50 cm below ground level.

Table 76. Qualification of the root distribution on the basis of root length.

Soil layer (cm)	Root length (% of total) *deep*	*normal*	*shallow*
0-10	<50	50-65	>65
30-50	>17	7-17	<7

Shear resistance

Table 77 shows the quality classes of the shear resistance for 0-4 cm below ground level and table 78 shows them for 10-14 cm below ground level.

Table 77. Quality classes of shear resistance at a depth of 0-4 cm below ground level.

Quality class	Limits ($N.cm^{-2}$)	Valuation
1	> 70	very good
2	55 - 70	good
3	45 - 55	moderate
4	35 - 45	poor
5	< 35	very poor

Table 78. Quality classes of shear resistance at a depth of 10-14 cm below ground level.

Quality class	Limits ($N.cm^{-2}$)	Valuation
1	> 80	very good
2	65 - 80	good
3	55 - 65	moderate
4	45 - 55	poor
5	< 45	very poor

6.2.6 Statistics

ANOVA was used to explore separately the relationship between the dependent variables openness of the sward, ground cover, root density and shear resistance and the independent variables plant community and management (see also § 2.4). The data set of the openness of the sward appeared to be slightly skewed. Therefore, it was log10 transformed prior to the analysis. All other data sets were normally distributed.

Pearson product-moment correlation with two-tailed probabilities was used to determine the relation between openness of the sward, ground cover, shear resistance, root length and root weight.

6.3 RESULTS

6.3.1 Openness of the sward

Openness of the sward of the plant communities

For a description of the plant communities and their management see chapters 3 and 4. In all years the openness of the sward, expressed in mean size of the bare spots, was greatest in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) (table 79). In 1994 the openness of the sward of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III), the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) and the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) was significantly smaller than that of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II), the *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV) and the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). Figure 38 shows the openness of the sward of the 5 main plant communities in 1989, 1990, 1993 and 1994.

Table 79. Mean openness of the sward per plant community in 1989, 1990, 1993 and 1994. Homogeneous groups at $p<0.05$.

1989

Plant comm.	Openness (cm2)	Homogeneous groups
VI	2.56	a .
V	4.02	a .
I	4.84	a .
IV	5.11	a b
III	5.90	a b
II	8.89	. b

1990

Plant comm.	Openness (cm2)	Homogeneous groups
VI	2.72	a .
III	3.36	a .
V	4.46	a .
II	11.49	. b

1993

Plant comm.	Openness (cm2)	Homogeneous groups
VII	2.35	a . .
VI	3.16	a . .
III	4.44	a b .
I	4.97	a b .
V	5.87	. b .
IV	5.99	. b c
II	8.06	. . c

1994

Plant comm.	Openness (cm2)	Homogeneous groups
VII	2.26	a . .
VI	2.97	a . .
III	4.70	a . .
I	5.32	a b .
V	7.78	. b c
IV	7.90	. b c
II	10.21	. . c

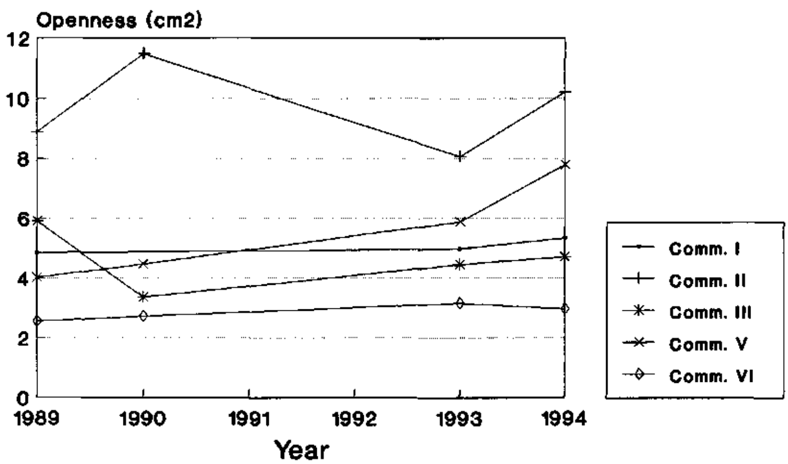


Figure 38. Openness of the sward in the 5 main plant communities in 1989, 1990, 1993 and 1994.

Size distribution of the bare areas

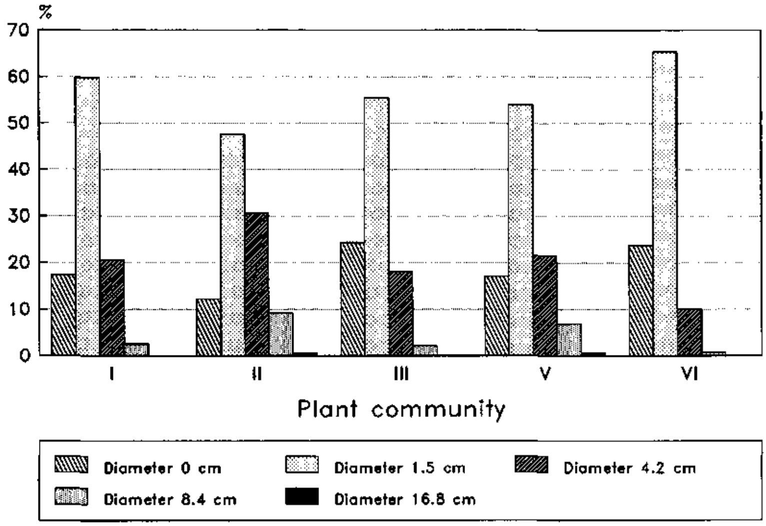


Figure 39. Size distribution of the bare areas per plant community in 1994.

Bare areas in the vegetation cover with a mean diameter of 1.5 cm were the commonest in all plant communities (figure 39). The biggest gaps with a mean diameter of 16.8 cm only occur in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) and the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). In these communities the frequency of bare areas with a mean diameter of 8.4 cm was also the highest: 9% and 7% respectively.

The *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) had the largest proportion of bare areas with a diameter exceeding 2.8 cm and the smallest proportion of bare areas with a diameter smaller than 2.8 cm (table 80). There seems to be a significant threshold between bare areas with a diameter smaller than 2.8 cm and bare areas with a diameter exceeding 2.8 cm.

Table 80. Size distribution of the bare areas per plant community in 1994. Homogeneous groups at p<0.05 level.

Diameter cm	Plant comm.	Proportion %	Homogeneous groups
0	III	24.3	a .
	VI	23.8	a .
	I	17.3	a b
	V	17.1	. b
	II	12.2	. b
0-2.8	VI	65.4	a . .
	I	59.8	a b .
	III	55.4	. b .
	V	54.0	. b .
	II	47.5	. . c
2.8-5.6	II	30.7	a . .
	V	21.5	. b .
	I	20.5	. b .
	III	18.1	. b .
	VI	10.1	. . c
5.6-11.2	II	9.2	a . .
	V	6.9	a b .
	I	2.5	. b c
	III	2.1	. . c
	VI	.8	. . c
11.2-22.4	II	.5	a .
	V	.5	a .
	I	.0	. b
	III	.0	. b
	VI	.0	. b

The proportion of bare areas with a diameter exceeding 2.8 cm was significantly higher in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) than in the other plant communities (table 81).

Table 81. Mean proportions of bare areas with a diameter larger than 2.8 cm per plant community. Homogeneous groups at p<0.05.

Plant community	Proportion %	Homogeneous groups
II	40.4	a . .
V	28.9	. b .
I	23.0	. b c
III	20.2	. . c
VI	10.8	. . c

Effect of management on the openness of the sward

In all years the sward was most open in permanent plots managed by burning every year and least open at grazing throughout the summer and at mowing in June with grazing in September, whereas grazing in June with mowing in September also showed a small openess in all four years (table 82).

Table 82. Mean openness of the sward (cm²) per management regime in 1989, 1990, 1993 and 1994. Homogeneous groups at p<0.05 level.

1989

Management	Openness (cm2)	Homogeneous groups
Gseas	1.84	a . . . .
M+G	2.42	a b . . .
G+M	2.65	a b . . .
1xM+r-lt	2.99	a b . . .
2xM+r	3.41	. b . . .
1xM+r-el	4.32	. b c . .
2xG	4.45	. b c . .
1xM+r/2y	7.07	. . c d .
2xM+-r	8.06	. . . d .
2xM-r	8.43	. . . d .
Burning	18.94	. . . . e

1990

Management	Openness (cm2)	Homogeneous groups
M+G	1.28	a . . .
Gseas	1.49	a b . .
G+M	2.55	a b c .
1xM+r-lt	2.80	. b c .
2xM+r	3.19	. . c .
2xG	3.21	. . c .
1xM+r-el	3.46	. . c .
2xM-r	8.91	. . . d
No manag	8.97	. . . d
2xM+-r	10.56	. . . d
1xM+r/2y	15.52	. . . d
Burning	16.66	. . . d

1993

Management	Openness (cm2)	Homogeneous groups
M+G	2.39	a . . .
Gseas	2.50	a . . .
G+M	3.13	a b . .
2xG	3.58	a b . .
2xM+r	4.05	. b . .
2xM+-r	4.89	. b c .
1xM+r-lt	5.73	. . c .
1xM+r-el	6.13	. . c .
2xM-r	7.22	. . c d
1xM+r/2y	8.26	. . . d
No manag	8.38	. . . d
Burning	9.82	. . . d

1994

Management	Openness (cm2)	Homogeneous groups
Gseas	2.22	a . . . .
M+G	2.45	a b . . .
G+M	2.47	a b . . .
2xG	4.88	. b c . .
2xM+r	5.23	. b c . .
1xM+r-lt	5.51	. . c . .
1xM+r-el	6.99	. . c d .
2xM+-r	7.74	. . c d .
2xM-r	8.62	. . . d .
1xM+r/2y	12.37	. . . . e
No manag	12.43	. . . . e
Burning	12.72	. . . . e

In 1990 the plots mown once every two years were almost as open as the plots with the burning management. In 1989 and 1993 the plots with management mowing once every two years were not mown. This resulted in a large openness of the sward in these plots in 1990 and 1994, whereas the opennes was much smaller in 1989 and 1993. In 1993 and 1994 the most open sward was found in the regimes mowing once every two years, no management and burning of the vegetation. In all years the sward mulched twice a year was significantly more open than the sward subjected to hay-making twice a year.

Figures 40 and 41 show the openness of the sward of 12 management regimes in 1989, 1990, 1993 and 1994.

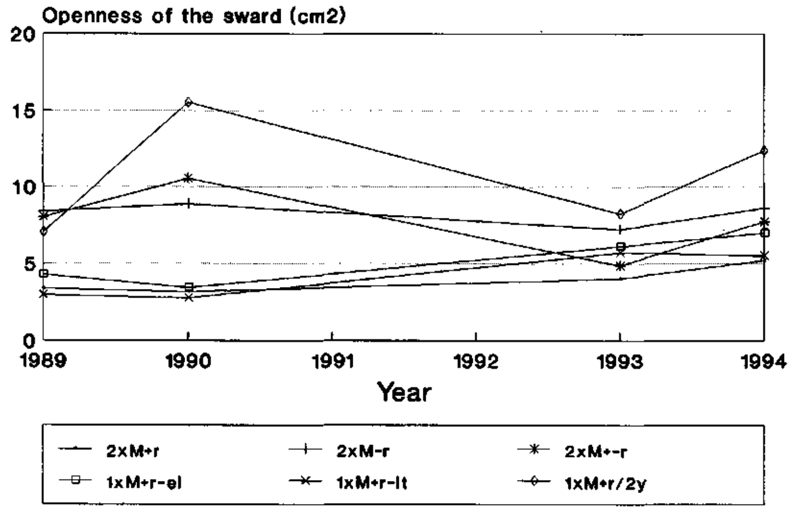


Figure 40. Openness of the sward for six mowing regimes.

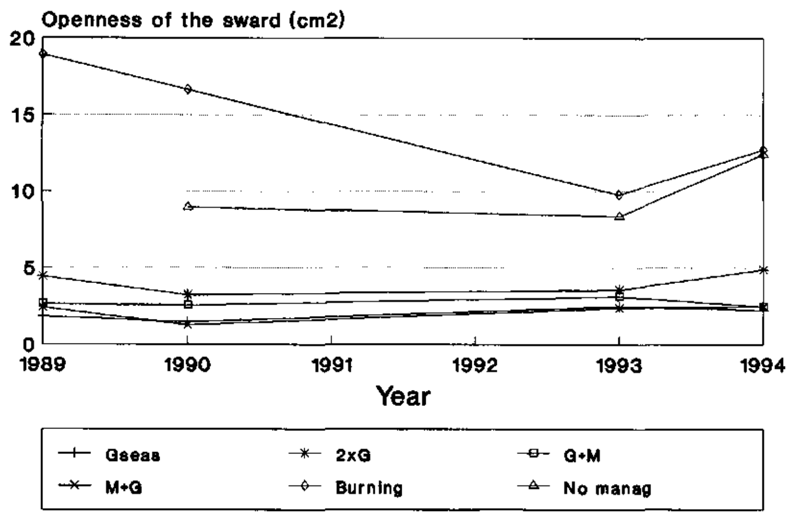


Figure 41. Openness of the sward for four grazing regimes and for burning and no management.

Size distribution of the bare areas
Bare areas with a mean diameter of 1.5 cm were commonest in all management regimes (figure 42). The biggest gaps with a mean diameter of 16.8 cm occurred only under the management regimes hay-making twice a year, hay-making in June with mulching in September, mulching twice a year, hay-making in September and hay-making one every two years. Under the management regimes burning and hay-making once every two years 13% of the bare areas had a mean diameter of 8.4 cm; under the no management regime 12% of the bare areas had a mean diameter of 8.4 cm. In the plots subjected to grazing throughout the season the maximum diameter of the bare areas was 4.2 cm, and in 31 of 100 cuts the pin touched a shoot (mean diameter of the pin 0.13 cm).

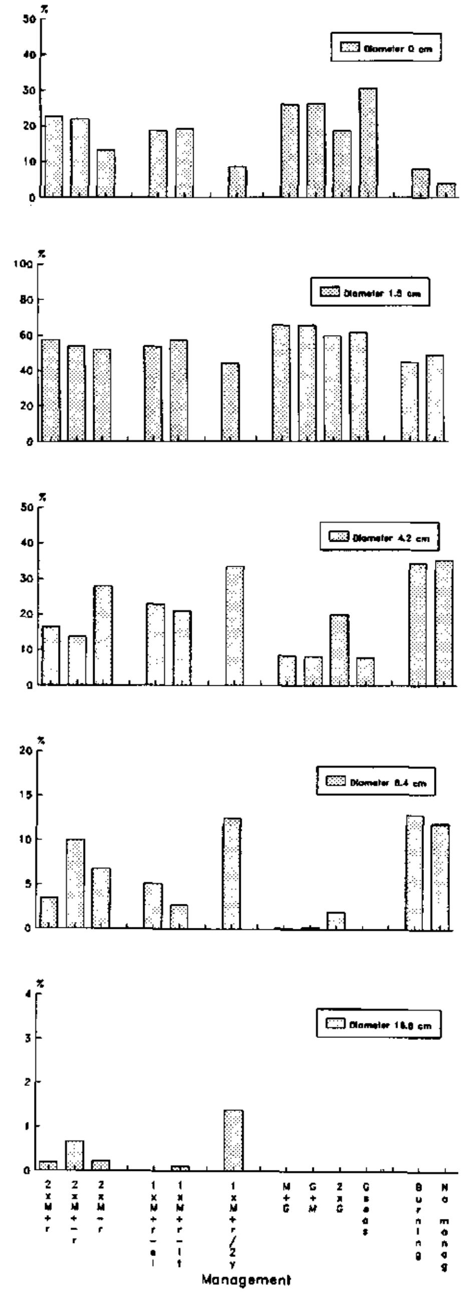


Figure 42. Size distribution of the bare areas per management regime in 1994.

Compared to the other management practices the proportion of bare areas with a diameter exceeding 2.8 cm was significantly higher under the management regimes burning, mowing once every two years and no management (table 83). The proportion of bare areas with a diameter exceeding 2.8 cm was significantly lowest in the management regimes grazing throughout the season, grazing in June with mowing in September, and mowing in June with grazing in September.

Table 83. Mean proportions of bare areas with a diameter exceeding 2.8 cm per management regime. Homogeneous groups at p<0.05 level.

Management	Proportion %	Homogeneous groups
Burning	47.5	a . . .
1xM+r/2y	47.4	a . . .
No manag	47.3	a . . .
2xM-r	35.1	. b . .
1xM+r-el	28.0	. b c .
2xM+-r	24.3	. b c .
1xM+r-lt	23.7	. . c .
2xG	22.0	. . c d
2xM+r	20.1	. . c d
M+G	8.6	. . . d
G+M	8.4	. . . d
Gseas	7.9	. . . d

6.3.2 Ground cover

Ground cover of the plant communities

Table 84. Mean ground cover per plant community in 1989, 1990, 1993 and 1994. Homogeneous groups at p<0.05.

1989 Plant comm.	Cover (%)	Homogeneous groups	1990 Plant comm.	Cover (%)	Homogeneous groups
III	76.6	a .	VI	79.5	a .
V	74.6	a .	V	77.5	a .
IV	74.0	a b	III	77.0	a .
VI	70.8	a b	II	51.7	. b
I	70.0	a b			
II	55.6	. b			

1993 Plant comm.	Cover (%)	Homogeneous groups	1994 Plant comm.	Cover (%)	Homogeneous groups
VII	78.4	a . .	VII	69.0	a . .
VI	71.4	a . .	VI	64.6	a . .
V	67.0	a b .	IV	60.9	a b .
IV	67.0	a b .	I	56.9	a b .
III	62.0	. b .	V	54.9	. b .
II	38.6	. . c	III	51.4	. b .
			II	34.0	. . c

In all years the ground cover was least in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) (table 84). In 1994 the ground cover of the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) and the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) was significantly greater than that of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) and the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V).

Figure 43 shows the ground cover of the 5 main plant communities in 1989, 1990, 1993 and 1994.

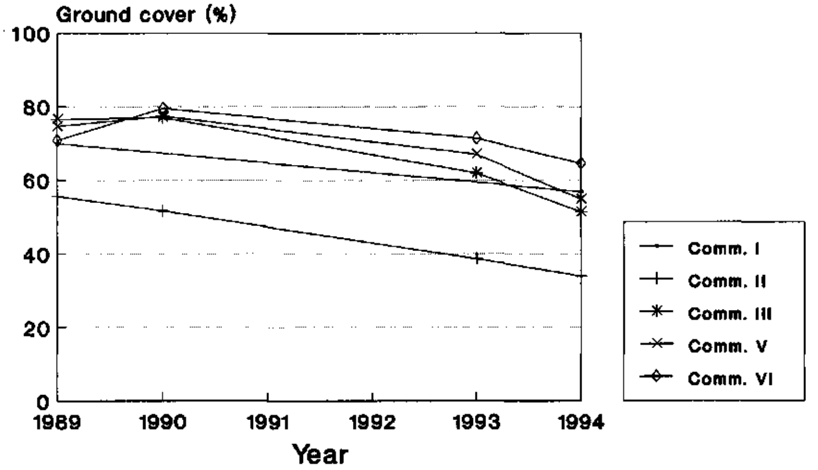


Figure 43. Ground cover in the 5 main plant communities in 1994.

Effect of the management on the ground cover

In 1993 and 1994 the ground cover was significantly greatest in the four grazing regimes and in mowing twice a year with removal of the hay (table 85). In 1994 ground cover was significantly smallest in the management regimes mowing once every two years, no management, and burning.

Table 85. Mean ground cover (%) per management in 1989, 1990, 1993 and 1994. Homogeneous groups at p<0.05 level.

1989

Management	Ground cover	Homogeneous groups
1xM+r-lt	83.7	a . . .
2xG	79.5	a . . .
M+G	76.5	a . . .
2xM+r	76.3	a . . .
Gseas	73.0	a b . .
G+M	68.0	a b . .
2xM-r	66.0	. b c .
1xM+r/2y	65.0	. b c .
2xM+-r	61.5	. . c .
1xM+r-el	56.0	. . c .
Burning	27.5	. . . d

1990

Management	Ground cover	Homogeneous groups
G+M	88.5	a . .
M+G	87.5	a . .
Gseas	86.5	a . .
2xG	82.3	a . .
1xM+r-lt	81.3	a . .
2xM+r	78.8	a . .
1xM+r-el	71.0	a b .
2xM-r	67.3	. b .
2xM+-r	55.0	. b c
Burning	43.0	. . c
No manag	41.0	. . c
1xM+r/2y	39.0	. . c

1993

Management	Ground cover	Homogeneous groups
M+G	74.4	a . . . . .
2xG	73.7	a . . . . .
Gseas	73.7	a . . . . .
G+M	70.5	a . . . . .
2xM+r	70.3	a . . . . .
2xM+-r	64.8	a b . . . .
1xM+r-lt	54.1	. b c . . .
1xM+r-el	50.2	. b c d . .
2xM-r	48.8	. . c d . .
1xM+r/2y	41.8	. . . d e .
No manag	30.8	. . . . e f
Burning	17.1	. . . . . f

1994

Management	Ground cover	Homogeneous groups
2xG	68.6	a . . .
G+M	67.2	a . . .
M+G	65.6	a . . .
Gseas	65.2	a . . .
2xM+r	64.8	a . . .
1xM+r-lt	56.2	. b . .
2xM+-r	55.2	. b . .
1xM+r-el	42.8	. . c .
2xM-r	40.4	. . c .
1xM+r/2y	28.9	. . . d
No manag	27.6	. . . d
Burning	20.1	. . . d

Figures 44 and 45 show the ground cover of 12 management regimes in 1989, 1990, 1993 and 1994.

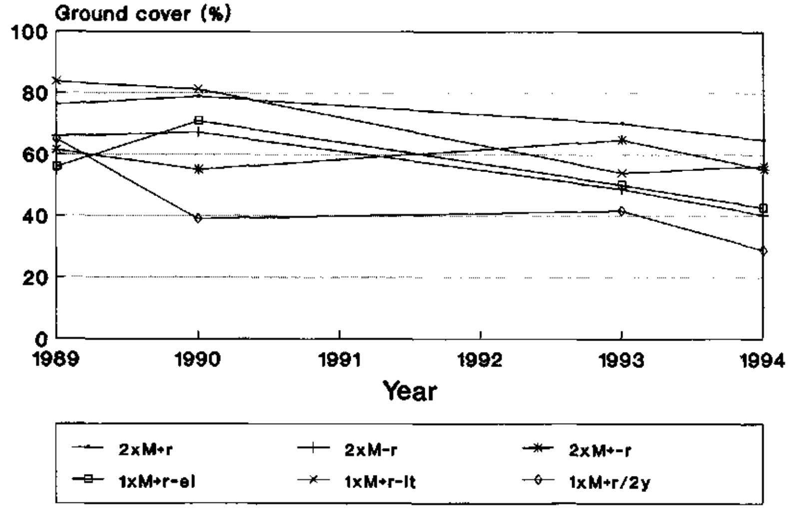


Figure 44. Ground cover (%) in six mowing regimes.

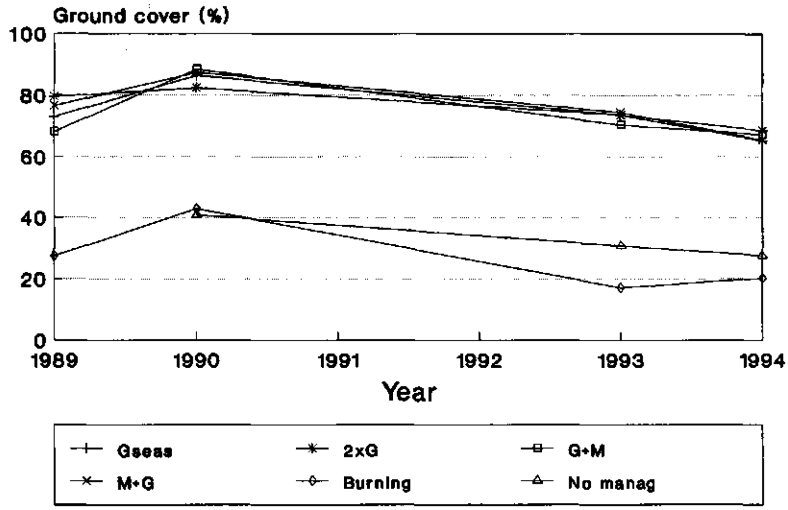


Figure 45. Ground cover (%) in four grazing regimes and in the burning and no management regimes.

6.3.3 Root density and root distribution

Root density of the plant communities

In 1994 the root length, the root weight and the specific root length were smallest in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) (table 86). Both the root length and the specific root length in this community were significantly smaller than in the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I). The root weight of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) was significantly smaller than in the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). Although the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) had a relatively small root weight, this community had the largest root length as a result of the relatively large specific root length.

Table 86. Root length, root weight and specific root length (SRL) per plant community in 1994. Homogeneous groups at $p<0.05$ level.

Plant comm.	Root length (m/5dm3)	Homogeneous groups	Plant comm.	Root weight (g/5dm3)	Homogeneous groups	Plant comm.	SRL (m/√g)	Homogeneous groups
I	817	a .	V	11.59	a .	I	95	a .
III	810	a b	III	11.53	a b	III	86	a b
V	746	a b	VI	11.28	a b	V	77	a b
VI	723	a b	I	9.58	a b	VI	76	a b
II	586	. b	II	8.45	. b	II	72	. b

Root distribution of the plant communities

In 1994 the root density in the upper 10 cm was always least in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) (see table 87). The root density from 0 to 3 cm was highest in the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI), but from 3 to 20 cm the root density was always highest in the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I). In contrast, this community had the least root density from 20 to 50 cm. Overall, the root density of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) was the best developed. The differences in the root weight per layer were less distinct so they will not be dealt with further here.

Table 87. Root density ($m.dm^{-3}$) per layer and per plant community in 1994. Homogeneous groups at $p<0.05$ level.

0-3 cm Plant comm.	Root length	Homogeneous groups	3-6 cm Plant comm.	Root length	Homogeneous groups
VI	928	a	I	460	a .
III	838	a	VI	458	a .
V	801	a	III	397	a .
I	719	a	V	384	a .
II	595	a	II	288	. b

6-10 cm Plant comm.	Root length	Homogeneous groups	10-15 cm Plant comm.	Root length	Homogeneous groups
I	285	a .	I	186	a .
III	239	a b	III	158	a b
V	207	. b	V	138	a b
VI	183	. b	II	117	. b
II	165	. b	VI	101	. b

15-20 cm Plant comm.	Root length	Homogeneous groups	20-30 cm Plant comm.	Root length	Homogeneous groups
I	148	a .	III	85	a . .
III	128	a b	II	59	a b .
V	112	a b	V	49	. b c
II	90	. b	VI	45	. b c
VI	76	. b	I	21	. . c

30-40 cm Plant comm.	Root length	Homogeneous groups	40-50 cm Plant comm.	Root length	Homogeneous groups
III	60	a .	III	52	a . .
II	50	a .	II	40	a b .
V	38	a .	V	27	. b c
VI	25	a b	VI	14	. b c
I	9	. b	I	9	. . c

Effect of management on root density

Table 88. Root length, root weight and specific root length (SRL) (depth 0-50 cm) per management in 1994. Homogeneous groups at p<0.05 level.

Management	Root length (m/5dm3)	Homogeneous groups	Management	Root weight (g/5dm3)	Homogeneous groups	Management	SRL	Homogeneous groups
2xM+-r	1176	a . . .	G+M	13.78	a .	2xM+-r	125	a . . .
M+G	884	a b . .	2xG	13.65	a .	M+G	94	. b . .
G+M	777	a b c .	1xM+r-el	12.33	a .	1xM+r-lt	84	. b c .
2xM+r	758	. b c .	2xM+r	12.24	a .	1xM+r/2y	83	. b c .
1xM+r-lt	747	. b c d	2xM+-r	11.33	a b	2xM+r	76	. b c .
2xG	737	. b c d	M+G	11.27	a b	2xM-r	75	. b c d
2xM-r	636	. b c d	No manag	10.84	a b	Gseas	74	. b c d
1xM+r-el	634	. b c d	1xM+r-lt	10.29	a b	G+M	74	. b c d
Gseas	626	. b c d	2xM-r	9.03	. b	2xG	70	. b c d
1xM+r/2y	609	. . c d	Gseas	8.68	. b	1xM+r-el	64	. . c d
No manag	493	. . c d	Burning	7.10	. b	No manag	53	. . . d
Burning	365	. . . d	1xM+r/2y	6.96	. b	Burning	48	. . . d

In 1994 the root length in the management practices hay-making in June with mulching in September and hay-making in June with grazing in September was significantly larger than in hay-making once every two years, no management and burning (table 88). Root length under hay-making twice a year was also significantly larger than in a burning management. In 1994 the root weights of grazing in June and mowing in September, grazing twice a year, mowing in June, and hay-making twice a year

Table 89. Root density ($m.dm^{-3}$) per layer per management regime in 1994. Depths: 0-3 cm, 3-6 cm, 6-10 cm and 10-15 cm. Homogeneous groups at p<0.05 level.

0-3 cm Management	Root length ($m.dm^{-3}$)	Homogeneous groups	3-6 cm Management	Root length ($m.dm^{-3}$)	Homogeneous groups
2xG	1143	a . .	2xM+-r	610	a . .
M+G	1020	a b .	2xG	469	a b .
G+M	976	a b .	M+G	440	a b .
Gseas	942	a b .	1xM+r-el	396	. b c
2xM+-r	922	a b .	2xM+r	391	. b c
2xM+r	827	a b .	1xM+r-lt	381	. b c
1xM+r-el	750	a b c	Gseas	377	. b c
1xM+r-lt	712	. b c	G+M	322	. b c
2xM-r	570	. . c	2xM-r	318	. b c
1xM+r/2y	544	. . c	1xM+r/2y	286	. b c
No manag	347	. . c	Burning	264	. b c
Burning	317	. . c	No manag	223	. . c

6-10 cm Management	Root length ($m.dm^{-3}$)	Homogeneous groups	10-15 cm Management	Root length ($m.dm^{-3}$)	Homogeneous groups
2xM+-r	396	a . .	2xM+-r	255	a . .
M+G	278	. b .	M+G	173	. b .
2xG	242	. b c	1xM+r-lt	151	. b c
2xM+r	221	. b c	2xM+r	150	. b c
1xM+r-lt	212	. b c	1xM+r/2y	141	. b c
1xM+r-el	211	. b c	2xM-r	125	. b c
2xM-r	169	. . c	G+M	113	. b c
1xM+r/2y	162	. . c	No manag	106	. b c
No manag	150	. . c	1xM+r-el	96	. b c
G+M	142	. . c	2xG	93	. b c
Gseas	134	. . c	Gseas	89	. . c
Burning	120	. . c	Burning	64	. . c

were significantly higher than that of mowing twice a year without removal of the hay, grazing throughout the season, burning, and mowing once every two years. In 1994 the specific root length in no management and in the burning management was significantly smaller than that of hay-making in June with mulching in September, hay-making in June with grazing in September, hay-making in September, hay-making once every two years and hay-making twice a year.

Effect of management on root distribution

In all four grazing regimes and in the regimes involving mowing twice a year with removal of the hay and with removal of the hay in June only the root density in the upper 3 cm was significantly higher than in mowing without removal of the hay, mowing once every two years, no management and burning (table 89). In the layer from 3-6 cm the root density was significantly higher in hay-making in June with mulching in September, grazing twice a year and hay-making in June with grazing in September when compared to no management (table 90). From 6-10 cm the root density in hay-making in June with mulching in September was significantly higher than in mulching twice a year, hay-making once every two years, no management, grazing in June with hay-making in September, grazing throughout the summer and burning. In the next 5 cm (10-15 cm) the root density in hay-making in June with mulching in September was still significantly highest while in burning and grazing throughout the summer it was significantly lowest. In the deepest layers (15-50 cm) the smallest root density was measured in grazing twice a year, hay-making in June, burning and grazing throughout the summer while the highest root density was found in grazing in June with hay-making in September, hay-making twice a year and no management. The differences in the root weight were less distinct so they will not be dealt with further here.

Table 90. Root density ($m.dm^{-3}$)per layer per management regime in 1994. Depths: 15-20 cm, 20-30 cm, 30-40 cm and 40-50 cm. Homogeneous groups at p<0.05 level.

15-20 cm

Management	Root length ($m.dm^{-3}$)	Homogeneous groups
2xM+-r	214	a . . .
M+G	143	a b . .
2xM-r	123	. b c .
1xM+r-lt	120	. b c .
2xM+r	114	. b c .
1xM+r/2y	112	. b c d
No manag	93	. b c d
G+M	84	. b c d
Gseas	61	. . c d
Burning	56	. . c d
1xM+r-el	52	. . . d
2xG	46	. . . d

20-30 cm

Management	Root length ($m.dm^{-3}$)	Homogeneous groups
G+M	111	a .
2xM+r	74	a .
No manag	58	a b
M+G	54	a b
1xM+r-lt	52	a b
2xM+-r	50	a b
1xM+r/2y	48	a b
2xG	43	a b
2xM-r	42	a b
Burning	36	a b
1xM+r-el	21	. b
Gseas	17	. b

30-40 cm

Management	Root length ($m.dm^{-3}$)	Homogeneous groups
G+M	71	a .
No manag	64	a .
2xM+r	51	a .
1xM+r-lt	47	a b
2xM+-r	44	a b
1xM+r/2y	36	a b
M+G	36	a b
2xM-r	31	a b
Burning	28	a b
2xG	23	a b
1xM+r-el	13	a b
Gseas	10	. b

40-50 cm

Management	Root length ($m.dm^{-3}$)	Homogeneous groups
G+M	47	a .
2xM+r	43	a .
No manag	38	a b
1xM+r-lt	37	a b
2xM+-r	34	a b
1xM+r/2y	31	a b
M+G	24	a b
2xM-r	23	a b
Burning	18	a b
1xM+r-el	10	. b
Gseas	9	. b
2xG	8	. b

Qualification of the root distribution

Root length samples qualified as having a deep root system only occurred in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) and in the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) (see table 91). In these communities about a quarter of the samples could be assigned to this category. Most of the root systems of the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) were qualified as shallow: more than 65% of the total root length was found in the upper 10 cm. Deep root systems only occurred in four of the mowing regimes and in the no management regime (table 92). In unmanaged dike grasslands all samples consisted of deep root systems. In contrast, grazing twice a year and grazing throughout the season led to a shallow root system.

Table 91. Pattern of root distribution (in root length). Proportion of root samples (%) as distributed over the classes (shallow, normal and deep) per plant community (see also table 76).

Plant community	Root length *shallow*	*normal*	*deep*
I	17	83	.
II	9	64	27
III	.	100	.
V	15	60	25
VI	67	33	.

Table 92. Pattern of root distribution (in root length). Proportion of root samples (%) as distributed over the quality classes shallow, normal and deep per management regime (see also table 76).

Management	Root Length *shallow*	*normal*	*deep*
2xM+r	.	90	10
2xM-r	.	67	33
2xM+-r	.	100	.
1xM+r-el	33	67	.
1xM+r-lt	17	50	33
1xM+r/2y	.	80	20
Gseas	67	33	.
2xG	100	.	.
G+M	.	100	.
M+G	33	67	.
Burning	.	100	.
No manag	.	.	100

6.3.4 Shear resistance

Shear resistance of the plant communities

In 1994 the shear resistance at 0-4 cm depth was greatest in the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) and smallest in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) (table 93). The shear resistance at depth 10-14 cm was significantly ($p<0.05$) smaller in the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) and the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) than in all other communities.

Tabel 93. Shear resistance at depths 0-4 and 10-14 cm per plant community in 1994. Homogeneous groups at $p<0.05$ level.

Depth 0-4 cm Plant comm.	Shear resistance	Homogeneous groups	Depth 10-14 cm Plant comm.	Shear resistance	Homogeneous groups
VI	55.9	a . .	VII	71.9	a .
IV	54.7	a b .	IV	67.0	a .
VII	53.5	a b .	VI	64.6	a .
III	48.5	. b .	III	61.3	a .
V	47.8	. b .	V	61.1	a .
I	43.2	. b c	II	46.0	. b
II	35.4	. . c	I	42.0	. b

Effect of management

The shear resistance at depth 0-4 cm was relatively great in the four grazing regimes, hay-making twice a year and hay-making once a year in June or in September (table 94). Mulching twice a year, burning, mowing once every two years and no management led to a small shear resistance. Differences were less distinct at depth 10-14 cm. The shear resistance at this depth was greatest in grazing in June and mowing in September and in mowing twice a year with removal of the hay. Mowing once every two years, burning and no management led to the smallest shear resistance.

Table 94. Shear resistance at depths 0-4 cm and 10-14 cm per management regime in 1994. Homogeneous groups at p<0.05 level.

Depth 0-4 cm			Depth 10-14 cm		
Management	Shear resistance (N/cm^2)	Homogeneous groups	Management	Shear resistance (N/cm^2)	Homogeneous groups
2xG	58.8	a	G+M	65.3	a . .
G+M	55.9	a b	2xM+r	65.1	a . .
Gseas	54.3	a b c . . .	2xG	63.0	a b .
M+G	53.5	a b c . . .	1xM+r-lt	62.6	a b .
2xM+r	51.3	. b c . . .	1xM+r-el	60.8	a b c
1xM+r-lt	50.6	. b c . . .	M+G	59.0	a b c
1xM+r-el	48.5	. b c . . .	Gseas	58.1	a b c
2xM+-r	44.9	. . c d . .	2xM+-r	54.6	a b c
2xM-r	39.5	. . . d . .	2xM-r	52.0	. b c
Burning	38.3	. . . d e .	1xM+r/2y	48.7	. . c
1xM+r/2y	33.4	. . . . e .	Burning	46.6	. . c
No manag	22.4	. . . . . f	No manag	42.1	. . c

6.3.5 Assessing quality on the basis of estimation classes

Plant communities

The quality of five different plant communities with respect to openness of the sward, ground cover, root length and shear resistance is given in table 95. Only the five main plant communities in 1994 are considered here (i.e. communities I, II, III, V and VI).

Table 95. Classification of the plant communities into quality categories (+ = good, 0 = moderate, - = poor, -- = very poor). For determining overall qualification: + = 1; 0 = 0; - = -1 and -- = -2.

Plant comm.	Openness of the sward	Ground cover	Root density (length)	Root distrib. (length)	Shear resist. 0-4 cm	Shear resist. 10-14 cm	Overall qual.
I	0	0	+	-	-	--	-3
II	--	-	-	0	-	-	-6
III	+	0	+	0	0	0	2
V	-	0	0	0	0	0	-1
VI	+	+	0	-	+	0	2

The communities can be ordered according to overall quality from good to poor as follows:

1. *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III)
2. *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI)
3. *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V)
4. *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I)
5. *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II)

Management regimes

The quality of the grasslands under different management regimes with respect to openness of the sward, ground cover, root length and shear resistance is given in table 96. In this table the different management practices are ordered according to overall quality from good to poor. From this it is concluded that grazing in June in combination with hay-making in September is the best management regime, followed by hay-making twice a year and hay-making in June with grazing in September. Burning the vegetation is the worst management regime, followed by no management and mowing once every two years.

Table 96. Classification of the management practices into quality categories (++ = very good, + = good, 0 = moderate, - = poor, -- = very poor). For determining overall qualification: ++ = 2, + = 1, 0 = 0, - = -1 and -- = -2.

Management	Openness of the sward	Ground cover	Root density (lengh)	Root distrib. (length)	Shear resist. 0-4 cm	Shear resist. 10-14 cm	Overall qual.
G+M	++	+	+	0	+	+	6
2xM+r	0	+	+	+	0	+	4
M+G	++	+	+	-	0	0	3
2xG	+	+	0	--	+	0	1
Gseas	++	+	0	--	0	0	1
1xM+r-1t	0	0	0	0	0	0	0
2xM+-r	-	0	++	0	-	-	-1
1xM+r-el	0	-	0	-	0	0	-2
2xM-r	-	-	0	+	-	-	-3
1xM+r/2y	--	--	0	+	--	-	-6
No manag.	--	--	-	++	--	--	-7
Burning	--	--	--	0	-	-	-8

6.3.6 Relation between openness of the sward, ground cover, root density and shear resistance

The openness of the sward is negatively correlated to the ground cover, the shear resistance and the root length ($p<0.001$) (see table 97). The ground cover by the vegetation is positively correlated to the shear resistance ($p<0.001$), the root length ($p<0.001$) and the root weight ($p<0.01$). The shear resistance is positively correlated to the root length ($p<0.001$).

*Table 97. Pearson correlation coefficients between openness of the sward, ground cover, shear resistance, root length and root weight. Minimum pairwise number of cases is 43. Two-tailed significance: * = $p<0.01$; ** = $p<0.001$.*

Correlations	Openness	Ground cover	Shear resist.	Root length
Ground cover	-.5974**			
Shear resist.	-.5628**	.6643**		
Root length	-.6503**	.6222**	.5515**	
Root weight	-.2351	.3901*	.3715	.5415**

6.4 Discussion

6.4.1 Openness of the sward and ground cover

Plant communities

Openness of the sward and ground cover appeared to be related to the plant communities. In 1994 the least openness and the greatest ground cover were measured in the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) (only the five main plant communities in 1994 are considered here; i.e. communities I, II, III, V and VI). The *Arrhenatheretum elatioris* with *Urtica dioica* and *Valeriana officinalis* (II) had by far the most openness and the least ground cover. There was a striking difference between the openness and the ground cover of the *Arrhenatheretum elatioris* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III): the openness was second best whereas the ground cover was second worst.

Effect of method of reconstruction

The comparison of the openness of the sward and the ground cover of experimental plots of different methods of reconstruction but with the same management regime (i.e. mowing twice a year with removal of the mowings) revealed that the age of the plots also plays a role. In 1990 the experimental plots completed in 1987 appeared to be more open and had less ground cover than the experimental plots reconstructed in the same way but completed in 1986 (Liebrand, 1993).

Irrigation directly after replacing the topsoil led to faster development of the vegetation with less openness of the sward and more ground cover in the first year after the reconstruction (Liebrand, 1993).

The openness of the complete sods replaced by hand was relatively high and the ground cover relatively small. The soil research showed that the replaced sods had the highest percentage of clay of the whole experimental dike. This high clay content led to a relatively large biomass, which adversely influenced the openness of the sod and the ground cover.

The vegetation development was slowest on the imported clay. Hence the openness was relatively high and the ground cover relatively low in comparison with the other methods of reconstruction.

Effect of sowing

The sowing of an annual grass species, in this case *Lolium multiflorum*, led to less openness of the sod and more ground cover in the years immediately after sowing (Liebrand, 1993). But sowing the standard grassland mixture BG5 led to more openness of the sward and less ground cover.

Effect of management

According to Thierry *et al.* (1958) management should consist of intensive grazing by sheep to achieve resistant swards. Both Huisman (1976) and Thierry *et al.* (1958) assumed that only frequent mowing would give the same result; the sward should be managed like lawns. If these two management regimes had been rigorously applied, the semi-natural species-rich grasslands on the river dikes of the Netherlands would have disappeared.

The results of some recent studies (Sýkora & Liebrand, 1987; van der Zee, 1992) have thrown another light upon on the matter. They found that the ground cover of species-rich grasslands appeared to be at least as good as that of swards grazed by sheep. Both soil fertility and management were found to be very important. Open swards were especially likely on nutrient-rich soils, whereas well closed swards mostly occurred on less nutrient-rich or nutrient-poor soils. In general, the biomass production is high on nutrient-rich soils. According to de Vries and Kruijne (1960) a larger biomass means a more monotonous herb layer and a less compact sward, which is prone to damage. Productive dike grasslands are mostly grazed. Livestock can severely damage dike grasslands. The resistance to livestock trampling rapidly decreases under wet conditions. In productive pastures the proportion of English ryegrass *Lolium perenne* is usually high. Swards with a high proportion of English ryegrass *Lolium perenne* are sensitive to frost damage.

On average, the sward of haylands is more open than swards grazed by sheep. The reason is that there is more variation in hayland types than there is in pastures grazed by sheep. Consequently there is more variation in sward openness in haylands. For instance well-managed species-rich haylands on a nutrient-poor soil are far less open than badly managed species-poor haylands on a nutrient-rich soil (van der Zee, 1992).

In the present research the method of reconstruction and the sowing appeared to affect the openness of the sward and the ground cover the most in the first three years after the reconstruction. Although the effect of the management also began immediately after the reconstruction, it did not become decisive until after three years (Liebrand, 1993).

Comparison of the results of the different management regimes within the different methods of reconstruction showed that the management is of great importance to the openness of the sward and the ground cover. After five years the least openness and the most ground cover was found in the grazing regimes, closely followed by haymaking twice a year. In pastures with only sheep grazing there are always spots that are grazed less intensively. These spots are susceptible to ruderalization (i.e. dominance of tall herbs). Their sward will be of less good quality, they will be more open and have less ground cover. Other spots will be overgrazed. In general, this will lead to sward damage. In pastures with sheep grazing in combination with haymaking in June or in September, there is less chance of ruderalization. In the management regime mowing in June and grazing in September, grazing should not be too intensive or last too long, otherwise there is a risk of the sward being damaged just before winter when it cannot regenerate because the growing season has stopped. The mowing management regimes showed more variation in openness and ground cover. The sward mulched twice a year was more open than that used for haymaking twice a year. The mowings left behind suffocated the vegetation, giving rise to bare spots in the sward. In addition to the removal of the mowings the mowing frequency is important for the openness of the sward and the ground cover. The most openness and the least ground cover were measured on swards used for haymaking once every two years (in autumn), especially in the spring following the year in which there had been no mowing. The least openness and the most ground cover was measured on swards used for haymaking twice a year. Haymaking only once a year in June led to more openness of the sward and less ground cover than haymaking once a year in September. In the autumn the unmown vegetation prevents light from penetrating further into the vegetation, which causes the openness of the sward to increase and the ground cover to decrease. Removing the biomass produced in summer seems essential to minimize the openness of the sward and promote the ground cover in the following spring. Burning, no management and mowing once every two years led to much openness of the sward and very little ground cover.

6.4.2 Root density and root distribution

The root density and distribution depend on the following environmental attributes of the soil:

1. moisture content,
2. texture/granular composition,
3. temperature,
4. nutrient level,
5. land use,
6. light reaching the surface,
7. acidity.

In general, these attributes influence the density and the distribution of the root system in the following ways (Braun-Blanquet, 1928; Klapp, 1971; Kutschera, 1960; Kutschera, 1966; Kutschera & Lichtenegger, 1982; Kutschera-Mitter, 1984):

Dryness (deep water table, rain deficit, increased evaporation, accelerated runoff down a steep slope) leads to an increase of the density and the distribution of the roots because the roots have to search for the water actively. The degree of branching of the roots, the amount of lateral roots and the root length and also the root-shoot ratio all increase with increasing dryness. Deep, fast growing roots are well able to avoid superficial desiccation of the soil.

The root mass decreases when the soil is heavier. On sandy soil a dense and rich branched root system develops. In a heavy clayey soil the roots mainly follow the cracks between the clods. With a decrease of the pore volume and of the aeration of the soil the root growth is strongly inhibited, the roots are less branched, have fewer root hairs, penetrate less deeply and weigh less. However, their diameter is often much increased. The unfavourable influence of a lessened aeration is not only the result of oxygen shortage but also of an excess of carbonic acid gas/carbon dioxide. In most cases, a sharp transition between different soil horizons impedes root growth. The greater the differences between the horizons, the more difficult it is for the roots to pass the transition.

A relatively high soil temperature stimulates both the speed and the depth to which the roots ultimately penetrate. At higher temperatures the soil layer to 30 cm depth is rooted in 14 days while at lower temperatures this takes 30 days. Therefore, the deepest rooting is achieved in the warmest areas.

Nitrogen and also phosphorus and potassium and most trace elements benefit the growth of both the roots and the shoots. Fertilizing diminishes the root-shoot ratio because the growth of the above-ground parts of the plants is stimulated more than the growth of the below-ground parts. However, fertilizing raises the above-ground production of the vegetation, which again leads to a strong reduction in rooting. In general, root development is increasingly inhibited as the vegetation becomes more closed. When the fertilizing is followed by an intensification of grassland use, this brings about a diminished extent and depth of the root system. Prins (1976) shows clear indications that very high nitrogen fertilization can severely decrease rooting which severely weakens the sward and greatly increases the risk of a decay of the sward (see 't Hart, 1976).

Each use of the grassland means a sudden reduction of the active leaf surface and, owing to this, an immediate interruption or reduction of the root growth. The more intensive the use, the smaller the amount of roots (Jones, 1933; Whittaker, 1979). In intensively grazed pastures 90% of the root mass can be found in the first 5 cm of depth.

When mowings are not removed or when the grassland is not managed at all, a litter layer will form. This layer of organic material retains water and its effect on the root system is comparable with regularly occurring light rain showers. This leads to shallow rooting (Miller, 1983). The organic matter content also influences the rooting intensity. Organic matter gives the soil a crumbly structure (Kononova, 1961), enabling a dense root system to develop and allowing the roots to penetrate deeper into the soil. Good light conditions lead to a large production of assimilates in the soil. These assimilates favour root growth. Therefore, good light conditions stimulate the development of an extensive and deep root system. In general, less roots are formed in an acid soil than in a basic soil. Liming often leads to deeper root growth.

A well developed, species-rich vegetation with a great number of species of dry flood-plain grass-lands can be found on moderately dry, nutrient-poor, sandy to sandy-clayey basic soils, especially on warm sites with much solar radiation. The agricultural use is extensive and consists of mowing once or twice a year with removal of the mowings, or of extensive grazing. Fertilizing is infrequent or absent.

From the above it can be expected that a species-rich dry floodplain grassland with many herbs will have a well developed, extensive and deep root system.

Root density and root distribution of the plant communities

In 1994 the *Arrhenatheretum elatioris* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) had the best root density expressed in root length in the 0-50 cm layer, followed closely by the *Arrhenatheretum elatioris* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). The *Arrhenatheretum elatioris* with *Urtica dioica* and *Valeriana officinalis* (II) had the smallest root length. In the

0-3 cm layer the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) had the greatest root length and in the 3-6 cm layer it had the second greatest root length. In the deeper layers the root length of this community decreased strongly. This community is especially frequent under grazing regimes. The root length of the *Arrhenatheretum elatioris* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) was the best from 3 to 20 cm below the soil surface. The root length of the *Arrhenatheretum elatioris* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) was second best at a depth of 0 to 20 cm and best from 20 to 50 cm. From 0 to 20 cm depth, the *Arrhenatheretum elatioris* with *Urtica dioica* en *Valeriana officinalis* (II) had a relatively small root length.

In 1994 the *Arrhenatheretum elatioris* with dominance of *Alopecurus pratensis* (V) had the best root density expressed in root weight in the 0-50 cm layer, followed closely by the *Arrhenatheretum elatioris* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III). Again, in the 0-10 cm layer the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) had a relatively great root weight, whereas in the deeper layer it decreased sharply. Overall, the root weight of the *Arrhenatheretum elatioris* with *Urtica dioica* and *Valeriana officinalis* (II) was the lowest.

Effect of management on the root density and root distribution

In 1994 great differences in root length and root weigth were measured between the different management regimes. The combinations of mowing and grazing (M+G and G+M) and mowing twice a year with removal of the mowings both times and removal of the mowings only in June led to the best root length, whereas mowing once every two years, burning the vegetation and no management led to the worst root length. Grazing in June in combination with mowing in August, grazing twice a year, mowing once a year in June, and mowing twice a year with removal of the mowings led to the highest root weight, whereas it was lowest in the regimes of mowing without removal of the mowings, grazing throughout the summer, burning, and mowing once every two years. In the two grazing-only regimes, grazing throughout the season and grazing twice a year, 48% of the total root length occurred in the upper 3 cm. In the grazing twice a year regime as much as 80% of the total root length occurred in the upper 10 cm; this figure was 74% for grazing throughout the season. In the two combinations of grazing and mowing (M+G and G+M) these proportions were 35% and 38% in the upper 3 cm and 63% and 58% in the upper 10 cm. The lowest proportions were measured in the no management regime: 22% in the upper 3 cm and 47% in the upper 10 cm.

Relation between openness of the sward, ground cover, shear resistance and root density

There appeared to be clear correlations between the openness of the sward, the ground cover by the vegetation, the shear resistance and the root density in the 0-3 cm layer. As ground cover increased, the open spots in the sward decreased in size and the shear resistance and the root density increased. The shear resistance was positively correlated to the root length and less so to the root weight. Clearly, the root length is of more importance to the erosion resistance than the root weight.

6.4.3 Estimating the quality of openness, ground cover and root density

Plant communities

Only the five main plant communities in 1994 are considered here (i.e. communities I, II, III, V and VI). The overall qualification of the *Arrhenatheretum elatioris* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) was the best, directly followed by the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI). The overall qualification of the *Arrhenatheretum elatioris* with *Urtica dioica* and *Valeriana officinalis* (II) was the worst. The relatively bad overall qualification of the *Arrhenatheretum elatioris* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) is caused by the fact that the spared zone, in which this community was especially common, contained an appreciable percentage of pebbles. This is particularly important for the shear resistance, which was indeed very low.

Management regimes
In 1994 there were great differences in the overall qualifications of the different management regimes. The overall qualification of the combination of grazing in June and hay-making in September was the best, followed closely by hay-making twice a year, and hay-making in June in combination with grazing in the autumn. The management regimes of mowing twice a year with removal of the mowings only in June, hay-making once a year in June or September, grazing twice a year and grazing throughout the season had intermediate scores. The overall qualification of the management regimes of mulching twice a year, hay-making once every two years, burning the vegetation and no management was far worse.

6.5 Conclusions

Plant communities
The composition of the vegetation appeared to affect the civil engineering quality of the sward. In 1994 the openness of the sward of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III), the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) and the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) was significantly smaller than that of the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II), the *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV) and the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V). In 1994 the shear resistance at 0-4 cm depth was greatest in the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) and smallest in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II). In all years the ground cover was lowest in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II). Besides, in 1994 the root length, the root weight and the specific root length were smallest in the *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II). This species-poor community, occurring at bad management practices (see chapter 4), is not only worst with respect to nature value and species richness, but also with respect to the civil engineering quality of the sward.

Whereas the openness of the sward and the ground cover of the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) were qualified as good, most of the root systems were qualified as shallow: more than 65% of the total root length was found in the upper 10 cm. This community, mostly occurring under grazing regimes, indicates that, although the coverage of the ground is good, the civil engineering quality of the sward might be bad when regarding root density and root distribution.

The overall qualification of the *Arrhenatheretum elatioris* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) was the best, directly followed by the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI). The overall qualification of the *Arrhenatheretum elatioris* with *Urtica dioica* and *Valeriana officinalis* (II) was the worst. The relatively bad overall qualification of the *Arrhenatheretum elatioris* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) is caused by the fact that the spared zone, in which this community was especially common, contained an appreciable percentage of pebbles. This is particularly important for the shear resistance, which was indeed very low.

Management
In 1993 and 1994 the least open sward was found in the regimes of grazing throughout the season, hay-making in June with grazing in September, and grazing in June with hay-making in September. In 1993 and 1994 the ground cover was significantly highest in the four grazing regimes and in the hay-making twice a year regime.

In 1994 the root length at the management practices hay-making in June in combination with mulching in September and hay-making in June in combination with grazing in the autumn was significantly larger than at hay-making once every two years, no management and burning. Deep root systems only occurred in four of the mowing regimes and in the no management regime. In contrast, grazing twice a year and grazing throughout the season led to a shallow root system.

In the two grazing-only regimes, grazing throughout the season and grazing twice a year, 48% of the total root length occurred in the upper 3 cm. In the grazing twice a year regime 80% of the total root length occurred in the upper 10 cm and under grazing throughout the season 74%. In the two combinations of grazing and hay-making these proportions were 35% and 38% in the upper 3 cm and 63% and 58% in the upper 10 cm. The lowest proportions were measured in the no management regime: 22% in the upper 3 cm and 47% in the upper 10 cm. The shear resistance at depth 0-4 cm was relatively great in the four grazing regimes, hay-making twice a year and hay-making once a year in June or in September.

The overall qualification of the combination of grazing in June and hay-making in September was the best, followed closely by hay-making twice a year, and hay-making in June in combination with grazing in the autumn. The management regimes of mowing twice a year with removal of the mowings only in June, hay-making once a year in June or September, grazing twice a year and grazing throughout the season had intermediate scores. The overall qualification of the management regimes of mulching twice a year, hay-making once every two years, burning the vegetation and no management was far worse.

The final conclusion is that a management which leads to a species-rich vegetation with a high nature value also positively affects the civil engineering quality of the sward. Contrary to this, a management which leads to a species-poor vegetation with a low nature value also negatively affects the civil engineering quality of the sward.

CHAPTER 7

RESTORATION MEASURES: TWO EXPERIMENTS

7.1 INTRODUCTION

There are two alternative strategies by which plants may spontaneously (re)colonize a target site; either through the germination of seeds that have survived the reconstructing period dormant in the soil or through the dispersal of seeds produced by populations in neighbouring sites (Bakker & Olff, 1992). On many reconstructed river dike no appropriate seed bank is available, so all species have to arrive from the neighbourhood. The probability of seed arriving in a target area depends on factors such as the number of seed sources in the landscape and their distance to a target site, the production of seeds and the presence and efficiency of dispersal vectors such as water, wind, animals and humans (the latter includes machinery, cars, soil redistribution, etc.). So, in situations where soil seed banks have been depleted because of the rapid decay of buried seeds or the removal of the topsoil, seed dispersal is the only natural option to restock a target site with seeds. In general, the establishment of species by natural processes tends to be slow and stochastic. In natural and semi-natural ecosystem development, species invade slowly and can take advantage of the developing environment produced by physical and chemical changes that occur during succession. They can also take advantage, so to speak, of years when conditions for colonization are especially favorable. The establishment of species also depends on the source of propagules available in the vicinity. Since most grassland species have a limited dispersal capacity (Fenner, 1985; Van Dorp, 1996), the distances between seed sources and a target site are assumed to be of crucial importance.

If the desired species are not able to bridge the distance to the target site or if this overbridging takes too long, all measures to create a highly accessible biotope, for instance by optimal management, will not lead to positive effects. Given the expense of ineffective management practices, this raises the question of whether it should be allowed or is even necessary to bring back the desired species by active reintroduction after ameliorating the conditions of the habitat. In artificial restoration of species diversity the required species are introduced artificially and sown by ordinary agricultural techniques. The choice of species can be tailored to suit the ecosystem being reconstructed, including species suitable for early as well as late stages of ecosytem development. An important consideration here is the provision of micro-environments for establishment which are suitable, both chemically and physically, for the desired species. There are four methods of active reintroduction of species: 1) sowing, 2) strewing fresh mowings, 3) planting out seedlings or even adults, and 4) transplanting parts of vegetations. Reintroduction of individual species can be applied by sowing them or by planting them out. Sowing is preferred because planting out is in essence less natural than sowing. By planting out the germinating phase and the susceptible juvenile stage are avoided. This prevents the environment from selecting and therefore the natural succession can be disturbed. When reintroducting plant species by sowing, the seeds used should preferably come from proximate populations (i.e. original ecotype). Strewing fresh mowings can be applied when the simultaneous reintroduction of several plant species or even a whole community consisting of grass and herb species is desired. A disadvantage of this method is that at any given time only part of the species have produced seeds that are able to germinate. This disadvantage can be overcome by mowing and strewing the fresh mowings at different moments through the summer season.

Sowing and strewing fresh mowings are preferred as methods for reintroduction of plant species. Their advantage is that only the restrictions to the dispersion capacity are removed, whereas the other natural processes like germination and settling can take their normal spontaneous course. Besides, the soil is not disturbed.

Bakker (1989) identified two factors limiting the (re-)establishment of species. The first is the poor dispersal mechanism of many species and the second is the lack of gaps or safe sites (Harper, 1977; Green, 1983). In general, species with large seeds can grow through the established surrounding vegetation, but small-seeded species need gaps for their establishment. The occurrence of gaps is strongly determined by the management practices i.e. the timing and frequency of hay-making or the intensity of grazing. Two restoration measures which can be taken to accelerate the succession on reconstructed river dikes are tested in a field experiment: 1) sowing of separate desired species and 2) strewing of cut material of species-rich grasslands. In both methods of introduction the establishment of the introduced species depends primarily on the suitability of the habitat for germination. Experiment 1 is focussed on the germination and the establishment of the seedlings in relation to the structure of the vegetation, especially the presence of gaps or safe sites. Experiment 2 is merely aimed on the efficiency of the method of reintroduction.

7.2 Methods

Experiment 1: germination in bare spots and in undisturbed vegetation
The establishment of (re-)introduced species depends primarily on the suitability of the habitat for germination (Bakker, 1989). A germination experiment using 17 herbs occurring on river dikes was performed to examine the experimental dike's suitability for the reintroduction of plant species. Once seedlings of re-introduced species have emerged, their fate largely depends on the density of the sward. To ascertain whether the species preferred open spots or a closed vegetation, they were sown both in a bare spot of 25 x 25 cm (the size of a mole-hill) and in the undisturbed vegetation. The bare spots were created by removing all the vegetation including the roots. The sowing in the undisturbed vegetation was applied in a trial plot of 100 x 100 cm. On 28 October 1987 12 plant species were sown (see table 98). With the exception of *Centaurea scabiosa* all these species occurred on the reconstructed experimental dike or had probably grown there before the reconstruction. On 18 July 1988 the experiment was enlarged with 7 species, two of which had also been sown in the first part of the experiment. The experiment was carried out on a small part of the dike away from the trial fields. All species were sown in the upper part of a dike section with a southerly aspect and a slope of 1:2.

Experiment 2: reintroduction of species by strewing of cut material
If the collection of seeds is difficult or very time consuming, some cut material of a source vegetation could be transported and spread on a target site. Wells *et al.* (1981) found that hay obtained from floristically rich meadows in the UK contained seeds of dozens of species.

In 1993 in two extensive road verges with a species-rich *Arrhenatherion* vegetation in the Netherlands the cut material was collected and transported to a target location, a recently reconstructed river dike in the direct neighbourhood of the source location. The vegetation in the source location was analysed with the Tansley method. On each road verge the species composition was determined, including relative abundance and the phenological state of the individual species. The cut material was picked up carefully, using a plastic sheet under the hay cart to collect seeds falling from the cart. This method was very effective: a large amount of small particles mainly consisting of seeds of several plant species was collected in this way. At the same time it was picked up, the cut material was shredded. In general, these small pieces break down more rapidly than larger pieces, so do not have to be removed after the cut material has been strewn. Before the cut material was strewn the target location was sown with a standard sowing mixture D1 containing *Lolium perenne* (40%), *Poa pratensis* (25%), *Festuca rubra* (25%) and *Trifolium repens* (10%). The sowing density was kept relatively low (20 kg ha^{-1}) to allow natural succession. In addition to the cut material the material collected on the sheet was strewn by hand on the target location. To determine the effect of the strewing of cut material, part of the same dike where no material had been strewn (control location) was studied and used for comparison.

7.3 RESULTS

Experiment 1: germination in bare spots and in undisturbed vegetation

There were great differences in germination of the species, both in open spots (see table 98) and in undisturbed vegetation. In the undisturbed vegetation only *Knautia arvensis*, *Pimpinella major* and *Salvia pratensis* germinated. All the seedlings grew slowly. *Galium verum* appeared to germinate well but the seedlings remained small and weak for a relatively long period. In the second and third years after sowing the plants grew only moderately and reached a height of only 8 cm. In the third year a few specimens flowered but no seeds set. *Lathyrus tuberosus* germinated poorly and the seedlings appeared vulnerable to insect and snail attack. Initially, *Pimpinella major* germinated fairly well but the seedlings appeared to be vulnerable, especially to soil desiccation. *Salvia pratensis* germinated rapidly but only one seedling emerged in each part of the experiment. These seedlings appeared not to be resistant to insects and snails. *Thalictrum minus* germinated slowly but after a while had nevertheless produced a reasonable number of seedlings, though these remained small and weak for a long time. Only a few seedlings survived and they remained small and vulnerable until the end of the third year. This suggests that the soil conditions were not appropriate for this species; the clay content may have been too high. Initially, *Vicia tetrasperma* germinated well but the seedlings appeared to be unable to withstand the desiccation in summer. The seeds of *Origanum vulgare* germinated almost immediately and the germination percentage was relatively high. The seedlings appeared to be resistant to insects and snails (probably because of their spicy smell) and bad weather conditions. Nevertheless the number of seedlings decreased slowly. *Prunella vulgaris* seeds started germinating somewhat later. The seedlings of this species also appeared to be resistant to insects, snails and weather. In the course of time, the number of seedlings stabilized. The growth of the seedlings of *Origanum vulgare* and *Prunella vulgaris* was almost identical. The good development of the seedlings of these species can be attributed to the massive seedling emergence, which enables an optimal microclimate to develop in which the seedlings thrive. Both species were already flowering in the second year after

Table 98. Results of the germination experiment, showing numbers of seeds sown, numbers of seedlings on certain dates and numbers of individuals at the end of the experiment.

No.	Plant species	N seeds	1988													1989								1990			
			01	01	02	03	04	05	05	06	08	09	10	10	11	02	03	04	05	06	08	09	12	03	03	05	08
			13	27	15	29	16	3	18	30	23	15	4	31	30	9	23	12	9	13	22	14	18	7	29	25	9
1	Agrim eup	25	.	.	.	.	.	1	1	1	1	1	1	1	1	.	1	1	1	1	1	1	1	1	1	1	1*
2	Campa rap	100	40	40	21	15	20	9	2	1	2	11	4	2	.	.	.	.	.	.	.	.	.	.	.	.	.
3	Centa sca	25	.	1	1	7	7	6	6	6	6	7	6	3	5	3	4	4	3	3	4	4*	.	4	4	4	4*
4	Galiu ver	50	20	21	16	22	29	33	25	29	24	34	20	6	12	.	7	13	14	15	10	15	.	.	20	20	20*
5	Lathy tub	15	.	.	.	1	.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	1	.	1	.	.	.
6	Knaut arv	25	2	4	5	8	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10*	10+	4	10	10#	10*	10*
7	Ononi r-s	10	.	.	.	2	3	3	3	3	3*	3+	2	2	1	.	2	3	4	4	4*	4+	3	4	4#	4	4*
8	Pimpi maj	25	.	.	.	2	12	9	5	5	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
9	Salvi pra	25	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
10	Thali min	25	.	1	1	4	9	11	6	5	5	3	3	1	1	1	.	.	.	1	3	.	.	.	1	1	1
11	Verba nig	100	24	17	7	5	2	2	.	1	3	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.
12	Vicia tet	25	6	6	5	10	11	10	10	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
13	Knaut arv	10	sown on 18-07-1988								1	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
14	Origa vul	100	sown on 18-07-1988								90	85	90	70	70	55	30	55	35	30	30	30	30	40	45	40	40*
15	Picri hie	10	sown on 18-07-1988								6	6	6	5	6	5	5	6	5	3	3	3	5	1	1	2	1
16	Prune vul	50	sown on 18-07-1988								11	18	31	21	27	33	25	25	25	30	25	30	30	35	35	35*	35+
17	Salvi pra	10	sown on 18-07-1988								1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.
18	Sangu min	20	sown on 18-07-1988								.	.	.	.	.	.	13	7	13	8	6	6	10	8	7	7*	10+
19	Valer loc	8	sown on 18-07-1988								.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	.	.

(* = flowering, + = mature seeds, # = seedlings from seeds of adult plants in the germination experiment)

1 Agrimonia eupatoria; 2 Campanula rapunculus; 3 Centaurea scabiosa; 4 Galium verum; 5 Lathyrus tuberosus; 6 and 13 Knautia arvensis; 7 Ononis repens ssp. spinosa; 8 Pimpinella major; 9 and 17 Salvia pratensis; 10 Thalictrum minus; 11 Verbascum nigrum; 12 Vicia tetrasperma; 14 Origanum vulgare; 15 Picris hieracioides; 16 Prunella vulgaris; 18 Sanguisorba minor; 19 Valerianella locusta.

sowing and *Prunella vulgaris* even produced seeds in that year. *Picris hieracioides* germinated well and a number of seedlings grew fast and became relatively tall, crowding out the smaller and weaker specimens. However, ultimately the conditions appeared to be unsuitable for this species, as by 1991 all specimens had disappeared. *Sanguisorba minor* only germinated in spring 1989, suggesting that this species needs a cold stimulus. The germination percentage was fairly high and the seedlings appeared to be resistant to insects and snails. The mortality was low. Although the seedlings remained small for a long period, some specimens flowered in the second year after sowing and produced seeds. *Valerianella locusta* only germinated in spring 1989. The seedlings were small and weak and not resistant to insect and snail attack and desiccation of the soil.

Sustainability of the sown species
In 1994, seven and six years after the sowings, six species had survived: *Centaurea scabiosa*, *Knautia arvensis*, *Origanum vulgare*, *Prunella vulgaris* and *Sanguisorba minor* in the open spots and *Pimpinella major* in the undisturbed vegetation. Comparing to 1990 *Agrimonia eupatoria*, *Galium verum*, *Ononis repens ssp. spinosa*, *Picris hieracioides* and *Thalictrum minus* had disappeared, although most of them had been flowering in 1990. Clearly, species that re-appeared in only a small population after the reconstruction were vulnerable and still at risk of disappearing.

Experiment 2: reintroduction of species by strewing of cut material
In the source location 64 plant species were determined (see figure 46). In the first two years after the strewing of the cut material 23 of them (36%) were found in the target location where cut material had been strewn but not in the control location. 9 species were found in both the target and control locations. 32 species (50%) of the species of the source location did not appear in either the target or the control location. Either they were very scarce or they were not bearing seeds at the moment of mowing. The 9 species found exclusively in the control location were mainly annual pioneer species. The strewing of cut material clearly hampered the germination of these species in the target location. The mean diversities in the Braun-Blanquet relevés in the target and control locations were respectively 28 and 16 species. From this it can be concluded that the strewing of cut material had a positive effect on the reintroduction of species on a reconstructed dike.

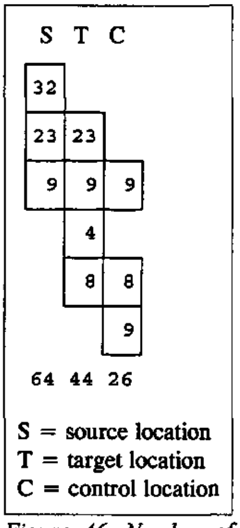


Figure 46. Number of species in the source, target and control locations.

7.4 DISCUSSION

Experiment 1: germination in bare spots and in undisturbed vegetation
This research was restricted to ascertaining whether the plant species in question germinate in a closed vegetation or whether they need bare spots to germinate and establish. Many grassland species produce seeds that only germinate in smaller or larger open spots in the vegetation (Brons, 1987). The seedlings in a closed vegetation have to cope immediately with competition from the species that are already present. In this case, the competition is for available light. The most important characteristic of an open spot in the vegetation layer is the ratio between the area and the height of the surrounding vegetation. This ratio largely determines the microclimate in the open spots (Lee, 1978). In shorter vegetation and in vegetation with less above-ground biomass more light generally penetrates to the soil surface where germination takes place. In a closed vegetation layer it is the above-ground biomass in particular that is crucial to the success of germination and probability of a seedling reaching maturity. Germination only takes place when there are 'safe sites' in the vegetation (Harper, 1977; Green, 1983). A safe site is characterized by stimuli for breaking the seed dormancy, conditions suitable for the germination process (for example favourable

light conditions), sufficient water and oxygen for germination and absence of predators, competition, toxic substances and pathogens.

Temperature and the quality of light are two important factors determining the germination (Grace, 1983). The germination response to different temperature regimes varies greatly between species. Higher temperatures favour the germination of some species but inhibit the germination of others. Some species germinate at low temperatures, but others do not. In some species, dormancy is broken by a fluctuating temperature. In others, it is broken by a cold treatment, and in some cases a cold treatment induces dormancy. Some plant species show a differentiation in the stimuli which are able to break dormancy. Often, the dormancy of only some of the seeds of a species is broken by a certain stimulus. For instance, some of the seeds germinate in autumn whereas the remainder do not germinate until the following spring. This mechanism helps spread risks.

The germination is also affected in various ways by the quality of the light (Brons, 1987). In some species there is a distinct relationship between the germination percentage and the ratio of red to far red light. In others, germination does not seem to be affected by the quality of the light. Germination can be inhibited by a low red to far red ratio under the canopy, especially in autumn, when the vegetation is still fairly closed. The green leaves filter out the red part of the sunlight, and therefore only light with a relatively low red to far red ratio reaches the soil, where it can inhibit the germination. In spring the vegetation is mostly so open that the effect of the red to far red ratio on the germination will be much smaller. Indeed, in spring the soil temperature and moistness are often more important than the light.

After one or more years the tallest and most vital specimens of most of the sown species in the two experiments appeared to have established in the open spots in the vegetation. This suggests that the absence of competition from plants surrounding the seedlings and the somewhat higher soil temperatures in the open spots (Brons, 1987) during the growth of the seedlings are more important than the presence or absence of specific germination attributes of the seeds. Only the seeds of *Pimpinella major* appeared to germinate better in the closed vegetation than in the open spots. No firm conclusion can be drawn about whether the presence of open spots is also important for the establishment of the young plants, because hardly any seeds germinated in the closed vegetation.

The six sown species present in 1994 (*Centaurea scabiosa*, *Knautia arvensis*, *Origanum vulgare*, *Prunella vulgaris* and *Sanguisorba minor* in the open spots and *Pimpinalla major* in the closed vegetation) were subjected to a management regime of mowing twice a year with removal of the mowings. This management probably caused *Agrimonia eupatoria* and *Ononis spinosa* to disappear. It seems that these species cannot tolerate relatively intensive management like this.

In general it can be postulated that the species in this experiment have three strategies of survival with regard to their generative propagation. The first strategy is the production of large amounts of seeds. Because of their very small size and their small reserves of food, the chance of these seeds successfully germinating and establishing is very small. This small chance of reaching maturity is compensated by the increased probability of one of these many seeds landing on a suitable location (i.e. safe site) than would be the case if there were fewer seeds. The second strategy consists of the production of only a small number of seeds which are resistant to the various adverse effects and thereby have a relatively good chance of germinating and establishing. This resistance is attributable to the large food reserves and tough seedcoat of these seeds. The reserves of food are particularly important in the period between the germination and the growth to a competitive adult. The third strategy is the production of a moderate number of seeds which have certain special attributes (spines, barbs, or one or more crowns of hairs) which enable them to be dispersed by animals or by wind. These special dispersal mechanisms increase the chance of the seeds reaching suitable locations to germinate and establish and thereby increase the chance of survival.

Experiment 2: reintroduction of species by strewing of cut material

Strewing fresh mowings can be applied when the simultaneous reintroduction of several plant species or even a whole community consisting of grass and herb species is desired. A disadvantage of this method is that at any given time only part of the species have produced seeds that are able to germinate. In the experiment only 50% of the species of the source vegetation germinated and established in the target location. This disadvantage can be overcome by mowing and strewing the fresh mowings at different moments through the summer season.

Recolonization starting sites

Restoration of species-rich grasslands can be brought about by using the RSS concept which is based on creating *recolonization starting sites* (RSS). A RSS may consist of a strip of ground with bare patches which is seeded with desired species or on which fresh mowings are strewn. Preferably, on dikes this strip should contain the whole gradient occurring on a dike to enable the sown species to select their own favourite new stand. Therefore, the breadth of the strip should equal the breadth of the dike. The length of the strip may vary from 10 to 40 or even 100 m. If seeded exclusively with seeds of herbs the RSS should also be seeded with a standard seed mixture or one or more grass species. The seeding density of the additional grass species should not exceed 20 kg ha^{-1} to allow natural succession. If fresh mowings are strewn no further seeding of grass species is necessary or required, since these mowings always contain several grass species. To get an optimal result the RSS should only be mown after all species have had the opportunity to flower and set seed. Preferably, parts of the target dike outside the RSS should also be seeded extensively with standard seed mixtures. Again, the seeding density should not exceed 20 kg ha^{-1}. Until the desired species have established on these parts of the dike they should be mown twice a year to obtain a well developed sod and, when necessary, to lower the biomass production to enable optimal germination and establishment of the species that spread from the RSS. After the desired species have established the management should be attuned to the fenology of these species.

Four major advantages of using the RSS concept are:

1. if a seed mixture appears to contain unwanted plant species, these can easily be removed even by hand. On river dikes such species include *Cirsium arvense*, *Cirsium vulgare*, *Rumex obtusifolius* and *Urtica dioica*,
2. the dispersal of species from the RSS can be studied,
3. when the sown species on a specific RSS have proved to form a well developed species-rich grassland, seeds or the fresh mowings can easily be obtained and used to create a new RSS,
4. the management of the relatively small RSS can differ from the management on the remaining part of the dike. The RSS should only be mown after all species have had the opportunity to flower and set seed whereas the remaining part of the target location is mown twice a year to obtain a well developed sod and, when necessary, to lower the biomass production to enable optimal germination and establishment of the species that spread from the RSS.

One should always keep in mind that all methods of reintroduction are emergency measures and that from a nature conservation point of view they may not nor cannot be a substitute for the protection and preservation of natural habitats and their specific species composition. Besides, all methods of reintroduction should be performed exclusively by experts. Lack of knowledge about the natural dispersion area of the species can lead to falsification of the flora. Sykora *et al.* (1993) define flora falsification as: the sowing or planting out of plant species outside their natural dispersion area or the sowing or planting out within the natural dispersion area of plant species with a genetic composition of deviating origin (e.g. wrong ecotype), or on stands where they should never appear naturally.

CHAPTER 8

RESTORATION OF SEMI-NATURAL, SPECIES-RICH GRASSLANDS ON RECONSTRUCTED RIVER DIKES: GENERAL CONCLUSIONS

In order to be able to restore ecosystems, it is crucial to analyse three sets of related problems. The first set of problems is related to restoring the growing conditons appropriate for the plant species selected; the *suitability*. The second set deals with the availability of propagules (seeds, fruits, vegetative parts, bulbs); the *accessibility*. The third set of problems contains the *sustainability* of the community. Attention has to be paid to the influence of competition as a critical factor in restoration practice.

This thesis is a feasibility study of restoring endangered species-rich plant communities on reconstructed river dikes. There are two basic approaches to restoration of floodplain grasslands: upgrading an existing degraded grassland and establishing the community on sites that lack species of floodplain grasslands. Actually restoring the original communities means restoring *diversity, species composition* and *ecosystem function.*

8.1 Suitability of river dikes

The starting point on river dikes must be the soil. Its properties and situation are crucial to the degree to which an ecosystem can develop naturally on the site, how far this development will progress and what treatments are necessary to assist its development. The large variation in ecological factors caused by increased spatial variation is responsible for the high species diversity on Dutch river dikes. The various aspects and inclinations of the dike slopes, the various soil types they are made of, and the material used for paving the top of the dike are all of ecological importance for the vegetation (Sýkora & Liebrand, 1987; Sýkora *et al.*, 1990; Van der Zee, 1992). From the top to the foot of a dike there is a gradient from dry to moist. At the same time the soil at the foot is often more nutrient-rich than the relatively nutrient-poor soil on the top, as a result of the direct and indirect agricultural influence at the foot of the dike and the eutrophication of the river water during high water periods and of the water in the adjacent ditches. Both situations are favourable for species diversity (Van Leeuwen, 1966, 1967, 1968). Additionally, various parts of the dikes are treated in different ways, which also gives rise to great differences in species composition and diversity.

On river dikes the suitability for species-rich grasslands containing rare species depends primarily on the fertility of the soil. The fertility of the soil is determined by the granular composition and the management of the vegetation. Within the granular composition the clay content plays an important role. To enable a species-rich vegetation on river dikes the clay content of the top layer (0-50 cm) should not exceed 25% (Sýkora & Liebrand, 1987; Van der Zee, 1992). Really floristically-rich vegetation with many rare species is only found on locations with <20% clay.

With respect to the clay content of the slopes of river dikes, it looks as if there is a reason to worry. In 1996 the Directorate General for Public Works and Water Management (Anon., 1996) prescribed a maximum sand (soil particles >63 μm) content of 40% in order to achieve topsoils with sufficient erosion resistance, corresponding to a sand (soil particles >50 μm) content of 43% (according to Van der Zee, 1992). Since there is a clear relationship between the clay and sand content in soil used for river dikes, a minimum clay content of 24% can be deduced. This minimum clay value strongly diminishes the floristic potential of river dikes reconstructed in conformity with the specifications mentioned above. The potential charge of slopes of river dikes should be taken in account when prescribing a maximum sand content. Conceivably, the landside of river dikes may contain a higher sand content and thus a lower clay content, allowing the development of a species-rich vegetation with high nature conservation interest.

However, a low clay content is not a guarantee for a species-rich vegetation, since the management also evidently affects the habitat. The mean clay content of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III), the second best developed plant community after the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I), was the highest. As a result of optimal management the peak standing crop of the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) was smaller than of most other communities, although they had lower clay contents. So, within the range of clay contents on the experimental river dike, the development of species-rich grassland vegetation is possible even on the heaviest clay, but only under optimal management practices. Manuring or leaving the cut material leads to accumulation of soil nutrients which raises the above-ground biomass. Consequently, a large above-ground biomass hampers the development of a species-rich vegetation.

Methods of reconstruction

The suitability of a target site can be artificially improved by using different restoration techniques. One such technique is to replace the former topsoil in situ, which in the past has proved to be suitable for the establishment of a species-rich vegetation. The new top layer should be at least 30 cm thick, but 50 to 60 cm is even better. Since the reconstructed river dikes are much broader than the old ones and thus the surface area has greatly increased, it is recommendable to replace the former top layer that was 60 cm thick as the new top layer that is 30 cm thick. To prevent the upper layer (0-30 cm) that contains most propagules from mixing with the deeper layer (30-60 cm) which contains hardly any propagules, it is recommended to store the upper layer away from the deeper layer and use the material of the upper layer on locations which have a good chance of developing a species-rich vegetation (i.e. the upper part of south-facing slopes). Seed rain from these parts will cause species to spread to the other parts of the reconstructed dike.

So, in reinforcing and reconstructing river dikes, it is becoming mandatory for surface soils to be conserved and replaced. In extreme cases, the soil crumb structure that normally builds up over a long period by natural processes can be damaged to such an extent in the restoration process that rooting is restricted. The finishing-off phase of the new slope of the dikes is important in this respect. One of the last activities is to compact the upper layer with heavy machines. If the compaction is too severe, rooting is greatly restricted and the development of the vegetation is severely retarded. Although more work is needed in this area, there is already sufficient evidence to make it clear that the relationship between soil structure and rooting depth is of considerable ecological significance. Further, sharp transitions between soil layers with different granular composition should be avoided, since roots are often unable to pass through them.

After applying special methods of reconstruction like transplantation of complete sods an optimal management is required to make this method of reconstruction succeed. On replaced sods, a negative change from a relatively species-rich vegetation to a species-poor vegetation took place. Whereas in 1987 all plots on the replaced sods were assigned to the species-rich *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III), in 1994 all plots except the plot with management hay-making twice a year were assigned to the species-poor *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II). This emphasizes the need of an optimal management after applying expensive methods of reconstruction like transplantation of complete sods.

Restoration management

The negative relationship between nutrient availability, above-ground biomass production and species richness is widely acknowledged (Grime, 1979; Vermeer & Berendse, 1983; Olff & Bakker, 1991). In this study the total number of species and the number of herb species were inversely correlated with the above-ground biomass in June. On eutrophic soils species-rich communities can only be established after nutrient impoverishment until a mesotrophic level has been achieved. Nutrient impoverishment can be achieved by hay-making without manuring or fertilization. Apart from directly affecting the structure of the sward (Bakker, 1987), hay-making influences the nutrient cycle, especially by removing the minerals accumulated in the standing crop (Bradshaw, 1980; Wells, 1980; Oomes, 1990). In this study nitrogen was actually removed under hay-making twice a year, hay-making in June with mulching in September, hay-making in June and hay-making in June with grazing in September. Under hay-making in September the amount of nitrogen removed was equal to the nitrogen input by atmospheric deposition. Mulching twice a year and hay-making once every two years led to nitrogen accumulation. Grazing results in hardly any nitrogen being removed and therefore, on clayey soils, grazing practices always lead to nitrogen accumulation. With the exception of mulching twice a year, under all management practices the amount of phosphorus removed exceeded the phosphorus input by atmospheric deposition. Potassium was actually removed by all mowing regimes except mulching twice a year. Generally, restoration management is accompanied by a dwindling standing crop and an increasing species-richness (Bakker & Olff, 1992). Therefore, management is an important tool in the restoration of species-rich grasslands.

On the basis of the results of some studies of the effect of restoration management on the biomass production and the diversity (e.g. Oomes & Altena, 1987), Oomes (1988) suggested a general pattern of the process of impoverishment consisting of four stages: 1) productivity decreases after stopping intensive land use with manuring, 2) changing competition between species; fast growing species dwindle and slower growing species increase, 3) production relatively low and canopy relatively open; increase of low-abundant species and germination and establishment of species out of the seed bank, and 4) germination and establishment of species from the neighbourhood that have arrived by dispersion. The soil can be impoverished by hay-making. Soil nutrients, especially nitrogen, phosphorus and potassium, are removed with the hay. For this reason, hay-making twice a year should be applied after the reconstruction for a period of one or two years (i.e. *restoration management*). Moreover, hay-making twice a year stimulates the development of a well-closed vegetation with a well developed root system (Sprangers, 1999). After these two years other management practices can be chosen; for example, hay-making once a year, extensive grazing during the summer season, intensive grazing during short periods imitating hay-making or hay-making in June or July in combination with grazing in August or September.

Although as much knowledge as possible is used to predict the target vegetation, there will always be successful and unsuccessful species. In general, species with large seeds can grow through the established surrounding vegetation, but small-seeded species need gaps for their establishment. The occurrence of gaps is strongly determined by the management practices i.e. the timing and frequency of hay-making or the intensity of grazing. It is difficult to say when a restoration has succeeded and when it has not. The success of the restoration may be considered by measuring the proportion of *target species* which is achieved after a certain period of time. The target species are based on the ecological potential of a habitat and together they frame a *target vegetation*.

Some species establish more readily than others, and some may appear in abundance in the early years of restoration, but later decrease or disappear. Species are considered to have established when they have reached the *minimum viable population* (MVP concept; Gilpin, 1987). This MVP varies greatly for different species. The duration of a restoration activity is considered to be the time required to reach a *dynamic equilibrium* (Cairns, 1987).

Generally, under optimal conditions it takes three to five years for a relatively species-rich grassland containing some floodplain species to be achieved (Liebrand, 1993a). Changes in vegetation - caused by succession - mainly occur immediately after a reconstruction; after a few years the changes proceed much more slowly. Although a relatively high species diversity was reached in part of the experimental plots and a number of rare to fairly common species occurred between 1987 and 1994, the succession of the main part of the vegetation of the recently reconstructed river dikes to species-rich, well developed, relatively stable grasslands containing many rare species will probably take several more years. In the first three to four years after a reconstruction the vegetation composition is merely determined by the method of reconstruction applied. Thereafter, the vegetation is closed and biomass has increased to a normal value with respect to the circumstances, for example the soil fertility. The management influences the biomass production and also the canopy structure. Therefore, from the fourth year after the reconstruction, the impact of the management on the vegetation composition and diversity begins to exceed the impact of the method of reconstruction applied.

8.2 Accessibility of river dikes

Different attributes can act as limiting factors in restoration succession or may hinder the rate of ecosystem development. They may be physical, chemical or biological. One of the most interesting is the biological factor of immigration. There are two alternative strategies by which plants may spontaneously (re)colonize a target site; either through the germination of seeds that have survived the reconstructing period dormant in the soil or through the dispersal of seeds produced by populations in neighbouring sites. The supply of suitable propagules is important in determining ecosystem development on reconstructed river dikes. Where the new substrate of the reconstructed river dikes is alien and very different from the natural soils of the immediate region, it is possible that the ecologically appropriate species are not present in the vicinity. In this situation the only species that will be able to colonize will be those with special powers of long-range dispersal.

Three restoration techniques aiming at a more or less spontaneous reintroduction of species can be applied when reconstructing river dikes. The first method is to *spare a (small) part of the original vegetation*. After the reconstruction the species of this vegetation spontaneously spread from the spared part to neighbouring parts of the dike. Since the dispersal capacity of most species is only small, sparing a part gives only a local effect. If sparing is not possible *transplantation of complete sods* bearing the original vegetation might be applied. Although adult plants might be introduced in an unsuitable habitat by transplanting complete sods, the dispersal of the species concerned to adjacent parts of the reconstructed dike is spontaneous and natural. This method should only be applied under strict conditions. Not only should the physical conditions (e.g. slope, aspect) change as little as possible but also the management should be the same after the sods have been replaced. The third method is the *replacement of the former topsoil* which contains different kinds of propagules (e.g. seeds, bulbs, tubers, rhizomes). This method can be applied by large machines which enables this method of re-introduction to be carried out on large areas like river dikes. Furthermore, the replacement of sods and former topsoil ensures that the new topsoil is suitable for the development of a species-rich vegetation (see also § 8.1 suitability of river dikes).

Between 1987 and 1994, seventeen stream valley species were found on the experimental dike. Only two of them, *Peucedanum carvifolia* and *Rumex thyrsiflorus*, were restricted to the spared zone immediately after the reconstruction. After 1987 they dispersed to bordering parts of the dike. The other species were also found in the replaced sods and on the replaced topsoil. This indicates the importance of the replaced sods and topsoil as a source of diaspores.

Almost all the species found in 1978 were also recorded in the first four years after the reconstruction. Only two species had not reappeared by 1994. A relatively large number of species was recorded in the period 1987-1994 but not in 1978. Clearly, the openness of the vegetation immediately after the reconstruction of the river dike offered many species a chance to germinate and establish temporarily or permanently in the vegetation. The seed sources were the seedbank and dispersion from nearby, by wind, on the mowing machines and on the fleece of the sheep. The management of the vegetation will determine whether these new species will remain or will slowly dwindle and disappear when the vegetation closes. In 1994, 50% of the 'new' species had already disappeared. Most of them were annuals.

Seed dispersal on river dikes

In general, the dispersal of diaspores of most species does not cover large distances (Harper, 1977; Ter Borg, 1979). Most of the seeds land near the parent plants. Verkaar *et al.* (1983) showed that the dispersal of diaspores of chalk grassland species barely exceeds 2 m. Bakker *et al.* (1995) focussed on seed dispersal by hay-making machinery. They found that the machinery contained 1000-1500 seeds per gram of adhering material. On the basis of this they estimated that transport by hay-making machinery could account for over 1.000.000 seeds. Sampling seeds from the skid disk before the machinery entered the field and after cutting that field showed that seeds from species dominant in the vegetation were actually exported. Seeds from species absent in the established vegetation were actually imported. Obviously, hay-making machinery plays a role in the dispersal of species. It is clear that the process of hay-making can contribute to the dispersal of seeds by machinery which moves from one hayfield to another. Whether the dispersed species establish or not depends, among other factors, on the density of the sward.

Bülow-Olsen (1980b) and Hilligers (1985) suggested putting large herbivores on species-rich grasslands and then on areas under restoration management in order to facilitate the dispersal of seeds of species with nature conservation interest. They both believed that livestock play a role in the dispersal of species. In a study of seed dispersal in a sheep-grazed mixed grassland Bakker (1989) concluded that viable seeds of several species which occurred in the grassland area had been transported to the heathland area via dung pellets and/or wool fragments. In several other studies viable seeds were found in dung of grazing cattle (e.g. Müller, 1955; Boeker, 1959). Geese pellets may also account for the spread of some plant species (De Vries, 1961; Bakker, 1989).

Reintroduction of species on river dikes

In many nature reserves and semi-natural areas one is trying to ameliorate the conditions of the habitats to stimulate the reappearance of lost species. One measure is to apply optimal management aiming at impoverishing of the soil. But if the desired species are not able to bridge the distance to the improved area or if this overbridging takes too long, this improvement of the biotope by optimal management will not lead to positive effects. Given the expense of ineffective management practices, this raises the question of whether it should be allowed or is even necessary to bring back the desired species by active reintroduction after ameliorating the conditions of the habitat. In artificial restoration of species diversity the required species are introduced artificially and sown by ordinary agricultural techniques. The choice of species can be tailored to suit the ecosystem being reconstructed, including species suitable for early as well as late stages of ecosytem development. An important consideration here is the provision of micro-environments for establishment which are suitable, both chemically and physically, for the desired species.

There are four methods of active reintroduction of species: 1) sowing, 2) strewing fresh mowings, 3) planting out seedlings or even adults, and 4) transplanting parts of vegetations. Reintroduction of individual species can be applied by sowing them or by planting them out. Sowing is preferred because planting out is in essence less natural than sowing. By planting out the germinating phase and the susceptible juvenile stage are avoided. This prevents the environment from selecting and therefore the natural succession can be disturbed. When reintroducting plant species by sowing, the seeds used should preferably come from proximate populations (i.e. original ecotype). Strewing fresh mowings can be applied when the simultaneous reintroduction of several plant species or even a whole community consisting of grass and herb species is desired. A disadvantage of this method is that at any given time only part of the species have produced seeds that are able to germinate. This disadvantage can be overcome by mowing and strewing the fresh mowings at different moments through the summer season. Complete sods can be transplanted when the conservation of complete parts of vegetations including the topsoil is desired, especially when one or more rare species are involved. Sometimes the complete sods are used not only because of the vegetation present but also because of the seed bank included. It can be risky to use the original topsoil because a great deal of the seeds in it are of ruderal species. Even topsoil from well developed species-rich hayfields often contains more seeds of ruderal species than of the desired perennial species of stable grasslands (Wells, 1983).

Sowing and strewing fresh mowings are preferred as methods for reintroduction of plant species. Their advantage is that only the restrictions to the dispersion capacity are removed, whereas the other natural processes like germination and settling can take their normal spontaneous course. Besides, the soil is not disturbed.

One should always keep in mind that all methods of reintroduction are emergency measures and that from a nature conservation point of view they may not nor cannot be a substitute for the protection and preservation of natural habitats and their specific species composition. All methods of reintroduction should be performed exclusively by experts. Lack of knowledge about the natural dispersion area of the species can lead to falsification of the flora. Sykora *et al.* (1993) define flora falsification as: the sowing or planting out of plant species outside their natural dispersion area or the sowing or planting out within the natural dispersion area of plant species with a genetic composition of deviating origin (e.g. wrong ecotype), or on stands where they should never appear naturally.

Recolonization starting sites
An explicit goal of the restoration could be to create *recolonization starting sites* (RSS concept) from where appreciated species can then spread to neighbouring areas, thereby accelerating the development of extensive species-rich grasslands. A RSS may consist of a strip of ground with bare patches which is seeded with desired species or on which fresh mowings are strewn. Preferably, on dikes this strip should contain the whole gradient occurring on a dike to enable the sown species to select their own favourite new stand. Therefore, the breadth of the strip should equal the breadth of the dike. The length of the strip may vary from 10 to 40 or even 100 m. If seeded exclusively with seeds of herbs the RSS should also be seeded with a standard seed mixture or one or more grass species. The seeding density of the additional grass species should not exceed 20 kg ha^{-1} to allow natural succession. If fresh mowings are strewn no further seeding of grass species is necessary or required, since these mowings always contain several grass species. Preferably, parts of the target dike outside the RSS should also be seeded extensively with standard seed mixtures. Again, the seeding density should not exceed 20 kg ha^{-1}.

Four major advantages of using the RSS concept are:
1. If a seed mixture appears to contain unwanted plant species, these can easily be removed even by hand. On river dikes such species include *Cirsium arvense, Cirsium vulgare, Rumex obtusifolius* and *Urtica dioica*,
2. the dispersal of species from the RSS can be studied,
3. when the sown species on a specific RSS have proved to form a well developed species-rich grassland, seeds or the fresh mowings can easily be obtained and used to create a new RSS,
4. the management of the relatively small RSS can differ from the management on the remaining part of the dike. The RSS should only be mown after all species have had the opportunity to flower and set seed whereas the remaining part of the target location is mown twice a year to obtain a well developed sod and, when necessary, to lower the biomass production to enable optimal germination and establishment of the species that spread from the RSS.

Increasing connectivity between isolated areas
Increasing the connectivity between isolated areas and decreasing the resistance to dispersing propagules and juveniles mean higher rates of (re)colonization as a result of increasing numbers of immigrants. In the contemporary Dutch agricultural landscape ribbon-like dikes and other ribbon-like biotopes like road verges can be of considerable ecological value. When managed in a proper way river dikes bearing species-rich vegetations with many rare species could function as a corridor between nature reserves and other areas important for the conservation of nature in the Netherlands. Insects in particular, but also small mammals and birds and probably also plant species take advantage of these longitudinal semi-natural elements in the landscape. According to Beeftink (1975) the dikes are important as plant migration routes between the 'river dunes' and terraces in the inland river valleys and the elevated sites of salt-marshes, dunes and rocky coasts on the seaside. Additionally, the small area-perimeter ratio enables river dikes to influence a relatively large bordering area. The ecological importance of river dikes justifies the effort and need for proper management and protection of species-rich dike grasslands.

8.3 Sustainability of semi-natural species-rich plant communities on river dikes

The river dikes in the Netherlands belong to the semi-natural landscape (Westhoff, 1952). Like other semi-natural landscapes such as meadows, dune grasslands, reed swamps and heaths, they are man-made natural ecosystems, their presence being the result of a very regular, continued management (Sýkora & Sýkora-Hendriks, 1977). This human activity in most cases meant a periodic removal of the vegetation by mowing, burning, cutting sods or grazing, and it has gone on for centuries, sometimes even for many centuries, in the same way. These, by modern standards primitive, agricultural activities, which were limited to relatively small areas and which varied from place to place, enabled a great diversity, a relatively fine-structured vegetation pattern and a large number of species-rich communities to develop on river dikes.

Nowadays, the deterioration in the semi-natural vegetation on river dikes has mainly been caused by the fact that they are increasingly being used for agriculture (fertilization, overgrazing, use of herbicides) but also because ecological features were insufficiently taken into account while reinforcing the dikes. Besides, the application of herbicides considerably reduced the number of species. And, like road verges, river dikes have a very small area-perimeter ratio which enables the adjacent arable land to affect mainly indirectly the vegetation through the use of artificial fertilizers (Sýkora & Sýkora-Hendriks, 1977).

Conservation management

Obviously, vegetation change can be manipulated by management, even under the unfavourable situation of long and narrow embankments (unfavourable area/perimeter ratio) bordering intensively used agricultural land. The time and frequency of cutting or grazing may be related to the growth of important species in the sward, whether to control dominant and aggressive grass species at the peak of growth or to allow rare plant species to complete their life cycle. Plant species must be able to produce seed occasionally. If management is inappropriate, the relatively expensive method of reconstruction replacing complete sods will be wasted labour because most of the species will still disappear.

With respect to the proportions in terms of percentages of either of the plant communities distinguished in this study, a general trend in the sequence of the management regimes can be seen. Hay-making twice a year is considered to be good management, hay-making in June with mulching in September, hay-making in September, hay-making in June and hay-making in June with grazing in September as moderate management, whereas mulching twice a year, hay-making once every two years in September, grazing throughout the summer, grazing twice a year, grazing in June with hay-making in September, burning of the vegetation and no management are considered to be bad management practices.

Because of the great importance of semi-natural elements in the landscape, the remnants of the old semi-natural vegetation types should be preserved against further destruction by a responsible environmental management and, additionally, the area of semi-natural vegetation types should be enlarged by appropriate restoration management.

However, since island biogeography theory (MacArthur & Wilson, 1967) and models of metapopulation dynamics (e.g. Gilpin & Hanski, 1991) suggest that the species richness of a habitat is maintained by a dynamic equilibrium between both local extinction and local colonization (Tilman, 1993), furthermore, it is likely that attempts to recreate species-rich grasslands on river dikes, by optimizing the management, will be most successful in a diverse landscape which can provide propagules of species for which the river dikes provide an opportunistic niche (Smith & Rushton, 1994).

8.4 Effect of the vegetation on civil engineering aspects of river dikes

The composition of the vegetation appeared to affect the civil engineering quality of the sward. The overall qualification of the well-developed, species-rich *Arrhenatheretum elatioris* with *Leucanthe-*

mum vulgare and *Lysimachia nummularia* (III) was the best, directly followed by the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI). The overall qualification of the species-poor *Arrhenatheretum elatioris* with *Urtica dioica* and *Valeriana officinalis* (II) was the worst. The relatively bad overall qualification of the *Arrhenatheretum elatioris* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) is caused by the fact that the spared zone, in which this community was especially common, contained an appreciable percentage of pebbles. This is particularly important for the shear resistance, which was indeed very low.

The overall qualification of the combination of grazing in June and hay-making in September was the best, followed closely by hay-making twice a year, and hay-making in June with grazing in September. The management regimes of mowing twice a year with removal of the mowings only in June, hay-making once a year in June or September, grazing twice a year and grazing throughout the summer had intermediate scores. The overall qualification of the management regimes of mulching twice a year, hay-making once every two years, burning the vegetation and no management was far worse.

So, during this research a positive relationship could be demonstrated between the vegetation composition and the civil engineering aspects of river dikes (see also Sprangers, 1999). The civil engineering quality of the sward was highest at the best-developed most species-rich plant community and lowest at the worst-developed most species-poor community. This emphasizes the need to restore species-rich grasslands (Sýkora & Liebrand, 1987; Van der Zee, 1992; Sprangers, 1996). Therefore, it can be concluded that both nature and civil engineering quality benefit from well-developed vegetations on river dikes, which can be achieved by taking the proper measures during the reconstruction and by applying optimal management thereafter. So, the final conclusion is that a management which leads to a species-rich vegetation with a high nature value also positively affects the civil engineering quality of the sward. Contrary to this, a management which leads to a species-poor vegetation with a low nature value also negatively affects the civil engineering quality of the sward.

EPILOGUE

The experimental dike was part of the river dikes controlled by the 'Groot Maas en Waal' Polder administration (i.e. Polderdistrict Groot Maas en Waal). It is gratifying to see that they have adopted some earlier advice and that they are already applying many of the techniques recommended in this thesis. In some of their reconstructions they have spared parts of the original vegetation and in others complete sods have been replaced. Further, the replacement of the former topsoil is now a standard procedure, especially on the land side of the dikes. They have also optimized the sowings on which occasion they moreover have differentiated between the riverside and the landside. In general, the upper zone of the land side slopes is sown nowadays with a seed mixture of grasses and herbs obtained in river floodplains in the neighbourhood of the reconstructed dikes. Additionally, management plans are made for all reconstructed river dikes, to ensure optimal management aiming at a vegetation with both a high nature conservation value and a high civil engineering quality. Long-term research on permanent plots is performed to describe, control and evaluate the further development of the vegetation.

I was delighted when the 'Groot Maas en Waal' Polder administration and the Province of Gelderland made it possible for me to write a brochure in which many practical recommendations based on the results of this research are given. This brochure 'Aanleg en beheer van rivierdijken: terugkeer van soortenrijk grasland door gerichte maatregelen' (Construction and management of river dikes: return of species-rich grassland by specific measures) has been widely available since May 1996 and is now used by many authorities responsible for the reconstruction and management of river dikes.

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SUMMARY

Up until 30 years ago a flower-rich grassland vegetation containing many species rare in the Netherlands used to be common on Dutch river dikes. However, the deterioration of the flora on dikes was already being reported at the end of the 1960s. Even then it was suggested that the use of fertilizer, herbicides and pesticides was causing the sharp decline in the number of species in this vegetation. At that time too, ecologists warned that the planned reinforcement of the dikes along the Rhine, Waal, Lek and IJssel would adversely affect the flora. They pointed out that it was very uncertain whether the specific dike flora with its many rare species would be able to recolonize the improved dikes, claiming that this would greatly depend on the material used to reinforce the dikes and on the measures taken to spare the existing flora. The gloomy forecasts of the fate of dike flora proved to be correct. Between 1968 and 1992 as much as 89% of the locations with a dry floodplain grassland vegetation in the Netherlands disappeared. In 1992 the vegetation of more than 90% of the river dikes consisted of species-poor grassland grazed by sheep, and rough vegetation mown for hay. Only about 7% of the surface area of the river dikes was covered by relatively species-rich grasslands of the phytosociological syntaxa *Arrhenatheretum elatioris* and *Lolio-Cynosuretum*, both belonging to the *Arrhenatherion elatioris*. Only 1% was covered by the typical species-rich dry-grassland *Medicagini-Avenetum*. The last remnants of those grasslands are currently at risk of disappearing. The deterioration in the semi-natural vegetation has mainly been caused by the slopes of the dikes increasingly being used for agriculture (fertilization, overgrazing, use of herbicides) but also because ecological features were insufficiently taken into account while reinforcing the dikes. The research project on the vegetation development on improved dikes was set up within this context.

In 1990 the government published the Nature Policy Plan, in which the term National Ecological Network was introduced. Essentially the National Ecological Network (NEN) comprises existing and future conservation areas and is built up out of core areas, nature redevelopment areas and connecting zones. The theory is that increasing the connectivity between isolated areas and decreasing the resistance to dispersing propagules and juveniles increases the numbers of immigrants and therefore the rates of (re)colonization. The long snaking form of river dikes, with a total length of 1002 km, makes them ideal zones for connecting core areas to nature redevelopment areas.

The Fluviatile district, mainly built up by the rivers, is one of the best characterized floral districts in the Netherlands. Dozens of species are either related or restricted to this district and to only one or a few other districts. These species are called *floodplain plants*. In the Fluviatile district the semi-natural dry floodplain grassland vegetation mainly grows on natural sandy river embankments and on artificial dikes.

In 1984 a research project was started to ascertain the optimum structure and growing conditions for the grass cover on river dikes. The conclusions drawn from this research project were that species-rich dry flood-plain grassland vegetation can only survive if certain conditions are met, not only with regard to habitat, but also with regard to management (Sýkora & Liebrand, 1987; van der Zee, 1992). The next step was to empirically test the feasibility of the ecological engineering measures proposed in the above mentioned projects. In the research project described in this thesis the core questions were whether the valuable, species-rich vegetation on the dikes can return after dike reinforcement and, if so, what are the preconditions for this during and after the reinforcement. This research project attempted to answer the following four questions. The first is more fundamental, the last three are very practical: (1) what is the relationship between the aboveground biomass, the vegetation structure, the soil fertility and the abundance of species, (2) is it possible to speed up the reappearance of species-rich dry floodplain grassland vegetation by replacing the original topsoil as the new toplayer after the reconstruction, (3) what is the effect of different seed mixtures and (4) given the different ways of re-establishing the dry floodplain grassland flora, which management strategy will lead to a favourable result in terms of ecological and civil engineering (i.e. high conservation value,

high erosion prevention capacity resulting from good ground cover and well-developed roots)? The research was carried out on the basis of data from 209 permanent quadrats divided over 125 trial fields. Each permanent quadrat has its own specific method of reconstruction, sowing and management.

In the period 1987-1994 9 plant communities were distinguished within the vegetation of the experimental river dike. Both the species composition and the abundance of the species differed between the plant communities. The *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) contained the most rare and less-common species. This community occurred only in the spared zone and in some plots directly bordering this zone. The *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III), the community with the highest species-richness and the second highest proportion of rare to less-common species, mainly occurred on replaced sods and replaced topsoil. The species-poor *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) appeared in 1990 only. Because of the relatively high proportion of nitrophilous tall herbs the appearance of this community indicated a certain degree of ruderalization. The *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV) appeared only sporadically and was almost disappeared by 1994. The *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) appeared in all methods of reconstruction. It was most common in 1994. The *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) and the association fragment of the *Arrhenatheretum* with *Phleum pratense* and *Ranunculus repens* (VII) appeared in all methods of reconstruction, except on replaced sods. Community VI mainly developed under grazing management. Community VII had almost disappeared by 1994. The pioneer stages, the fragmentary community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) and the fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) had already disappeared in 1990.

The plant communities can be classified as follows on the basis of method of reconstruction, management and successional stage: the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) is typical of the spared zone, the species-poor *Arrhenatheretum* with *Urtica dioica* and *Valeriana officinalis* (II) is a rough vegetation resulting from bad management, the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) is a species-rich grassland occurring with good and moderate management practices involving replaced sods and replaced topsoil, the *Arrhenatheretum* with dominance of *Alopecurus pratensis* (V) is an intermediate vegetation which will develop further either into a hayfield vegetation or into a pasture vegetation, depending on which management strategy is applied, the *Lolio-Cynosuretum* with *Crepis capillaris* and *Ranunculus repens* (VI) is a grassland vegetation strongly influenced by grazing and the *Arrhenatheretum* with *Leucanthemum vulgare* and *Trifolium pratense* (IV), the fragmentary community with *Matricaria maritima* and *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) and the fragmentary community with *Capsella bursa-pastoris* and *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) are pioneer stages, which had wholly or almost disappeared in 1994.

In the first two years after the reconstruction there was a great variance in the abundance of the pioneer species. However, in all methods of reconstruction the pioneer species dwindled rapidly and in course of time they almost disappeared. In 1990, four years after the reconstruction, differences in vegetation composition were still related to the differences in method of reconstruction. In 1994, eight years after the reconstruction, the *Arrhenatheretum* with *Peucedanum carvifolia* and *Rumex thyrsiflorus* (I) still mainly occurred in the spared zone but also in some permanent plots on replaced topsoil and on imported clay directly bordering the spared zone. Until 1992 the species-rich *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III) only occurred on replaced sods and replaced topsoil. In 1994 this community had also appeared on imported clay, but only on imported clay bordering the replaced sods. This implies that species dispersed from the spared zone and from the replaced complete sods to bordering plots. The proximity of the spared zone and the replaced sods seem have been crucial. Whether the vegetation in all methods of reconstruction will develop to the vegetation of the spared zone depends primarily on the soil composition. Since the soil differs in physical and chemical attributes, it is expected that the vegetation will never become similar to the vegetation in the spared zone. The development of the vegetation will also be determined by the slope and the aspect.

Eight years after the reconstruction the different methods of reconstruction still had different vegetation. The vegetation in the spared zone was still the best developed and contained the most less-common and rare species. The best way to assure maintenance of species-rich grassland vegetation on reconstructed river dikes is therefore to spare a strip or zone of this vegetation during the reconstruction. The species-rich vegetation in this spared zone functions as a source of propagules. Species disperse from here other parts of the dike and the redevelopment of the vegetation is stimulated. To ensure optimal results, the soil composition of those new parts should resemble the soil composition of the spared zone as much as possible. If it is not possible to save part of the original vegetation, the upper soil layer can be put aside as complete sods or as topsoil and can be replaced as the new topsoil after the reconstruction. Replacement of complete sods by hand appears to be useful for the conservation of populations of (rare) species. As this method is very expensive, it should only be applied on river dikes with a well developed vegetation and if it is impossible to spare a zone. If the valuable, species-rich floodplain grassland vegetation is to return, the habitat must be the same before and after the reinforcement of the dikes. Replacing the original topsoil after the reinforcement provides a topsoil of similar composition to that before the reinforcement. In this way the redevelopment of species-rich grasslands is promoted by previously occurring species re-establishing from the propagules present in the replaced topsoil. In 1994 the *Arrhenatheretum* with *Leucanthemum vulgare* and *Lysimachia nummularia* (III), the community with the greatest species-richness and the second highest proportion of rare to less-common species, still mainly occurred on replaced sods and replaced topsoil. Applying deeper soil as the new top layer gave the same results as using imported clay as the new top layer: both hamper the quick restoration of botanically valuable, semi-natural, species-rich grasslands. Propagules are very rare or even absent. Deeper soil should only be used as a top layer when its texture and chemical properties accord with the demands of the desired vegetation. The use of imported clay delays the redevelopment of the vegetation after a reconstruction. Imported clay should only be applied when no former topsoil or good quality subsoil are available.

The seed mixtures applied influence the development of succession. Former river dike grasslands redevelop fastest if seeded with D1+LGM (i.e. standard seed mixture plus locally gathered seed mixture). Applying locally gathered seed mixtures accelerates succession. If a species-rich grassland is present on a river dike, seeds should be collected and seed mixtures of the original vegetation should be composed before the dike reconstruction begins. The effect of sowing a locally gathered seed mixture is influenced by the composition of the source vegetation and the moment of gathering. Seed mixtures containing a considerable proportion of *Lolium perenne* seeds are unsuitable, as the redevelopment is retarded. These mixtures should not be applied, especially not at the high rates in order of 70 kg per ha which used to be common. Sowing an annual grass species like *Lolium multiflorum* or the standard seed mixture D1 at a low rate of 20 to 25 kg per ha did not seem to retard the development of a species-rich vegetation.

Ninety-eight percent of the plant species found before reconstruction reappeared after reconstruction. Most species reappeared on the replaced former top layer. Only a few (rare) species did not re-establish but were still present in the unmodified zone. Most relatively rare species occurred only in low numbers and consequently were still at risk of disappearing, especially in the absence of appropriate management. Given this risk, a spared zone seems to be the best guarantee for the conservation of the plant species after the reconstruction.

In the first years after reconstruction the influence of the methods of reconstruction and the seed mixtures applied appears to be preponderant. At this time the structure of the vegetation is quite open and the competition between species is low. When the vegetation closes, competition increases.

Subsequently, management of the vegetation can be used as an important means to regulate competition and consequently species composition. A species-rich vegetation only develops when managed properly.

Species richness was found to be determined not only by the soil composition and soil nutrient status but also by the above-ground biomass. Generally, at a lower biomass higher species-richness was measured. The above-ground biomass was strongly determined by the management applied. In 1994 hay-making twice a year led to the third lowest biomass and the highest species-richness.

Hay-making twice a year led to the highest erosion resistance measured in this research. The openness and the ground cover achieved by this management were as high as those achieved by the grazing practices applied in this research. In general, the openness was least and the ground cover was greatest in the grazing management. In contrast, root density and root distribution, especially the latter, were better in the management strategy involving hay-making twice a year than in the grazing strategies.

The best management practices in terms of erosion resistance features like openness of the sward, ground cover, root density and shear resistance appear to be grazing in June in combination with hay-making in September, hay-making in June in combination with grazing in September and hay-making twice a year. In this respect, grazing twice a year, grazing during the whole season, hay-making in September and hay-making in June in combination with mulching in September are moderate. Hay-making in June, mulching twice a year, hay-making once every two year, burning and no management are bad management practices.

The best management in terms of ecological features like species richness and number and proportion of rare species is hay-making twice a year. In this respect, hay-making in June in combination with mulching in September, hay-making in June, hay-making in September and hay-making in June in combination with grazing in September are moderate. The other grazing practices, mulching twice a year, hay-making once every two years, burning and no management are bad management practices.

SAMENVATTING

Tot dertig jaar geleden kwamen op de rivierdijken in Nederland nog uitgestrekte, bloemrijke stroomdalgraslanden voor die vele zeldzame soorten bevatten. Tegen het einde van de zestiger jaren werd er voor het eerst melding gemaakt van aantasting en achteruitgang van deze graslanden. Toen al werd gesuggereerd dat de snelle afname van de soortenrijkdom werd veroorzaakt door bemesting en het gebruik van herbiciden en pesticiden. Ook werd toen al door ecologen gewaarschuwd dat de geplande grootschalige dijkverbetering langs de Rijn, Waal, Lek en IJssel een negatieve uitwerking zou hebben op de dijkflora. Ze betwijfelden of de specifieke dijkflora met zijn vele kritische soorten in staat zou zijn de verbeterde dijken te herkoloniseren. Volgens hen zou dit grotendeels afhangen van het materiaal dat zou worden gebruikt bij de dijkverbetering en van de maatregelen die getroffen zouden worden om de dijkflora zoveel mogelijk te ontzien. De negatieve voorspellingen zijn uitgekomen. Tussen 1968 en 1992 is in Nederland 89% van de lokaties met een droog stroomdalgrasland verdwenen. In 1992 bestond meer dan 90% van de begroeiing op dijken uit soortenarme schapenweiden en ruige hooilanden. Slechts 7% van de oppervlakte van de dijken was begroeid met min of meer soortenrijke graslanden die worden gerekend tot de phytosociologische eenheden *Arrhenatheretum elatioris* en *Lolio-Cynosuretum* die beide worden gerekend tot het verbond *Arrhenatherion elatioris*. Slechts 1% was begroeid met het karakteristieke, soortenrijke droge stroomdalgrasland dat wordt gerekend tot het *Medicagini-Avenetum*. Momenteel dreigen ook de laatste restanten te verdwijnen. De sterke achteruitgang van deze halfnatuurlijke vegetatie is voornamelijk veroorzaakt doordat de dijkhellingen meer en meer werden gebruikt voor agrarische doeleinden, wat gepaard ging met bemesting, overbegrazing en het gebruik van herbiciden, maar ook doordat bij de dijkverbetering in het verleden onvoldoende rekening is gehouden met de ecologische waarden van de dijken. Vanuit deze wetenschap is dit onderzoek naar de vegetatie-ontwikkeling op verbeterde dijken opgezet.

In 1990 publiceerde de Nederlandse regering het Natuurbeleidsplan waarin de term Ecologische Hoofdstructuur werd geïntroduceerd. In essentie is de Ecologische Hoofdstructuur een samenhangend netwerk van bestaande en toekomstige natuurgebieden. De EHS bestaat uit kerngebieden, natuurontwikkelingsgebieden en verbindingszones. Verbetering van de verbindingen tussen geïsoleerde gebieden en opheffing van barrières voor de verspreiding van dieren en planten leiden tot een toename van (her)kolonisatie door een toenemend aantal nieuwkomers. Door de langgerekte vorm van de rivierdijken, met een totale lengte van 1002 km, zijn zij bij uitstek geschikt als verbindingszones tussen bestaande natuurgebieden en natuurontwikkelingsgebieden.

Het fluviatiel district, dat in hoofdzaak is ontstaan door toedoen van de grote rivieren, is een van de best gekarakteriseerde floradistricten van Nederland. Vele tientallen soorten komen uitsluitend of vrijwel uitsluitend in dit district voor. Deze soorten worden stroomdalplanten genoemd. In het fluviatiel district groeit het halfnatuurlijke, droge stroomdalgrasland voornamelijk op natuurlijke zandige oeverwallen en rivierduinen en op door de mens aangelegde dijken.

In 1984 is een onderzoeksproject gestart waarin de ecologische standplaatseisen en groeicondities van de dijkgraslanden is onderzocht. De belangrijkse conclusies van dit onderzoek waren dat soortenrijke, droge stroomdalgraslanden alleen voorkomen bij bijzondere omstandigheden, niet alleen met betrekking tot de standplaats maar ook met betrekking tot het beheer (Sýkora & Liebrand, 1987; van der Zee, 1992). De volgende stap was het onderzoeken van de toepasbaarheid van de, in de hierboven beschreven onderzoeken aanbevolen, ecologische uitvoeringsvoorschriften en -maatregelen in de praktijk. In het onderzoek dat in dit proefschrift wordt beschreven waren de kernvragen of de waardevolle, soortenrijke dijkvegetatie kan terugkeren na een dijkverbetering en, zo ja, aan welke voorwaarden hiervoor moet worden voldaan tijdens en na de dijkverbetering. In dit onderzoek is getracht een antwoord te geven op de volgende vier vragen. De eerste vraag was meer fundamenteel van aard, de laatste drie vragen waren vooral praktijkgericht: 1) wat is de relatie tussen de bovengrondse biomassa, de vegetatiestructuur, de bodemvruchtbaarheid en de soortensamenstelling, 2) is het mogelijk de terugkeer van soortenrijk stroomdalgrasland te versnellen door het terugzetten van de oorspronkelijke toplaag als de de nieuwe toplaag na de verbetering, 3) wat is het effect van verschillende inzaaimengsels en 4) welk beheer geeft bij de verschillende methoden van herstel van het droge stroomdalgrasland het beste resultaat met betrekking tot enerzijds de ecologie en anderzijds de civieltechnische kwaliteit van het dijkgrasland? Het onderzoek is uitgevoerd aan de hand van 209 permanente proefvakken verdeeld over 125 proefvelden. Elk permanent proefvak wordt gekarakteriseerd door een methode van aanleg, de toepassing van een bepaald inzaaimengsel en een bepaald beheer.

In de periode 1987-1994 zijn 9 plantengemeenschappen onderscheiden in de vegetatie op de proefdijk. De gemeenschappen verschilden zowel in soortensamenstelling als in de mate waarin de soorten aanwezig waren. Het *Arrhenatheretum* met *Peucedanum carvifolia* en *Rumex thyrsiflorus* (I) bevatte de meeste zeldzame en minder algemene soorten. Deze gemeenschap kwam alleen voor in de gespaarde zone en in enkele proefvakken die grensden aan deze zone. Het *Arrhenatheretum* met *Leucanthemum vulgare* en *Lysimachia nummularia* (III), de gemeenschap met de hoogste soortenrijkdom en het op-een-na hoogste aandeel van zeldzame tot minder algemene soorten, kwam voornamelijk voor op de teruggezette complete zoden en op de teruggezette zodegrond. Het soortenarme *Arrhenatheretum* met *Urtica dioica* en *Valeriana officinalis* (II) verscheen pas in 1990. Vanwege het relatief hoge aandeel van hoogopgaande nitrofiele ruigtkruiden duidt het verschijnen van deze gemeenschap op een zekere mate van verruiging. Het *Arrhenatheretum* met *Leucanthemum vulgare* en *Trifolium pratense* (IV) kwam gedurende de onderzoeksperiode slechts sporadisch voor en was in 1994 bijna verdwenen. Het *Arrhenatheretum* met dominantie van *Alopecurus pratensis* (V) kwam in alle methoden van aanleg voor. In 1994 was dit de meest voorkomende gemeenschap. Het *Lolio-Cynosuretum* met *Crepis capillaris* en *Ranunculus repens* (VI) en het association fragment van het *Arrhenatheretum* met *Phleum pratense* en *Ranunculus repens* (VII) zijn ook in alle methoden van aanleg aangetroffen, behalve op de teruggezette zoden. Gemeenschap VI kwam voornamelijk voor bij beweiding. Gemeenschap VII was in 1994 vrijwel verdwenen. De pionierstadia, de fragmentaire gemeenschap met *Matricaria maritima* en *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) en de fragmentaire gemeenschap met *Capsella bursa-pastoris* en *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) waren beide in 1990 al verdwenen.

Op basis van de methode van aanleg, het beheer en het successiestadium kunnen de plantengemeenschappen als volgt worden geclassificeerd. Het *Arrhenatheretum* met *Peucedanum carvifolia* en *Rumex thyrsiflorus* (I) is kenmerkend voor de gespaarde zone. Het soortenarme *Arrhenatheretum* met *Urtica dioica* en *Valeriana officinalis* (II) is een ruige vegetatie als gevolg van slecht beheer. Het *Arrhenatheretum* met *Leucanthemum vulgare* en *Lysimachia nummularia* (III) is een soortenrijk grassland dat is aangetroffen bij goed en matig beheer en wel op teruggezette zoden en op de teruggezette toplaag. Het *Arrhenatheretum* met dominantie van *Alopecurus pratensis* (V) is een intermediaire vegetatie die zich verder zal ontwikkelen, ofwel in de richting van een hooilandvegetatie, ofwel in de richting van een weilandvegetatie, afhankelijk van het beheer. Het *Lolio-Cynosuretum* met *Crepis capillaris* en *Ranunculus repens* (VI) is een graslandvegetatie die sterk is beïnvloed door begrazing. Het *Arrhenatheretum* met *Leucanthemum vulgare* en *Trifolium pratense* (IV), het *Arrhenatheretum* met *Phleum pratense* en *Ranunculus repens* (VII), de fragmentaire gemeenschap met *Matricaria maritima* en *Plantago major* [*Arrhenatherion/Chenopodion*] (VIII) en de fragmentaire gemeenschap met *Capsella bursa-pastoris* en *Poa annua* [*Eu-Polygono-Chenopodion*] (IX) zijn pionierstadia, die geheel of vrijwel geheel zijn verdwenen in 1994.

In de eerste 2 jaar na de dijkverbetering was er op de proefdijk een ruime variatie in de mate van aanwezigheid van de pioniersoorten. In alle methoden van aanleg nam het aantal pioniersoorten snel af en na verloop van tijd waren ze vrijwel verdwenen. In 1990, vier jaar na de dijkverbetering, waren de verschillen in vegetatiesamenstelling nog steeds toe te schrijven aan de verschillende methoden van aanleg. In 1994, acht jaar na de dijkverbetering, kwam het *Arrhenatheretum* met *Peucedanum* *carvifolia* en *Rumex thyrsiflorus* (I) nog steeds voornamelijk voor in de gespaarde zone maar ook in enkele proefvakken op de teruggezette toplaag en op aangevoerde klei die echter steeds grensden aan de gespaarde zone. Tot 1992 kwam het soortenrijke *Arrhenatheretum* met *Leucanthemum vulgare* en *Lysimachia nummularia* (III) alleen voor op teruggezette zoden en op de teruggezette toplaag. In 1994 werd deze gemeenschap ook aangetroffen op aangevoerde klei, maar alleen in proefvakken die grensden aan de teruggezette zoden. Dit geeft aan dat de soorten uit zowel de gespaarde zoden als de teruggezette zoden zich hebben verspreid naar aangrenzende proefvakken. De nabijheid van de gespaarde zone en de teruggezette zoden blijkt dus een cruciale rol te spelen bij de herontwikkeling van soortenrijk dijkgrasland. Of de vegetatie in alle methoden van aanleg zich zal ontwikkelen in de richting van de vegetatie in de gespaarde zone hangt op de eerste plaats af van de bodemsamenstelling. Omdat de bodem van de proefdijk verschillen vertoont in zowel de fysische als de chemische opzicht is de verwachting dat de vegetatie van de gehele proefdijk nooit geheel identiek zal worden aan de vegetatie in de gespaarde zone. Bovendien wordt de ontwikkeling van de vegetatie mede bepaald door de helling en de expositie van het dijktalud.

Acht jaar na de dijkverbetering verschilt de vegetatie van de verschillende methoden van aanleg nog steeds. Nog steeds is de vegetatie in de gespaarde zone het best ontwikkeld en is het aandeel van zeldzame en minder algemene soorten het grootst. De beste garantie voor het behoud van een soortenrijke graslandvegetatie op verbeterde rivierdijken is het sparen van een strook met deze vegetatie tijdens de verbetering. De soortenrijke vegetatie in deze gespaarde zone functioneert vervolgens als verspreidingsbron. De plantensoorten verspreiden zich hiervandaan en stimuleren op die manier de herontwikkeling van soortenrijk grasland op wel verbeterde delen van de dijk. Een optimaal resultaat wordt alleen bereikt wanneer de bodemsamenstelling van de wel verbeterde delen van dijk zoveel mogelijk overeenkomt met die van de gespaarde zone. Als het niet mogelijk is een deel van de oorspronkelijke vegetatie te sparen, is een andere mogelijkheid het apart houden van de oorspronkelijke toplaag in de vorm van complete zoden of van zodegrond en het terugzetten van dit materiaal als nieuwe toplaag na de dijkverbetering. Het met de hand terugzetten van complete zoden lijkt bruikbaar te zijn voor het behoud van populaties van zeldzame soorten. Het is echter een dure methode van aanleg die alleen moet worden toegepast op rivierdijken met een goed ontwikkelde vegetatie en waar het bovendien niet mogelijk is een deel ervan te sparen bij de verbetering. De waardevolle soortenrijke stroomdalvegetatie kan alleen terugkeren wanneer de standplaatsomstandigheden voor en na de verbetering min of meer gelijk zijn. Dit kan voor een deel worden bereikt door de oorspronkelijke toplaag in de vorm van zodegrond na de dijkverbetering terug te zetten als de nieuwe toplaag. Op deze manier wordt de herontwikkeling van soortenrijk grasland gestimuleerd door de hernieuwde vestiging van vroeger voorkomende soorten vanuit de vegetatieve en generatieve voortplantingsorganen die in de zodegrond aanwezig zijn. In 1994 kwam het *Arrhenatheretum* met *Leucanthemum vulgare* en *Lysimachia nummularia* (III), de gemeenschap met de hoogste soortenrijkdom en het op-een-na hoogste aandeel van zeldzame en minder algemene soorten nog steeds voornamelijk voor op de teruggezette zoden en de teruggezette toplaag. Het gebruik van de onderlaag als nieuwe toplaag geeft hetzelfde resultaat als toepassing van aangevoerde klei voor de nieuwe toplaag. Beide methoden van afwerking belemmeren een snel herstel van botanisch waardevolle, halfnatuurlijke, soortenrijke dijkgraslanden. Zowel vegetatieve als generatieve voortplantingsorganen ontbreken vrijwel geheel. De onderlaag kan alleen worden toegepast wanneer de textuur en de chemische eigenschappen ervan voldoen aan de voorwaarden van de gewenste vegetatie. Aangevoerde klei moet alleen worden toegepast voor de nieuwe toplaag wanneer de kwaliteit van de oorspronkelijke toplaag en de onderlaag niet voldoet.

De toegepaste inzaaimengsels beïnvloeden de vegetatie-ontwikkeling en de successie. Het herstel van het oorspronkelijke grasland verloopt het snelst bij inzaai met D1+LGM (i.e. standaard inzaaimengsel D1 in combinatie met een lokaal gewonnen zadenmengsel). Inzaai met een lokaal gewonnen zadenmengsel versnelt de successie. Wanneer op een rivierdijk soortenrijk grassland aanwezig is, wordt aangeraden hieruit zaden te winnen waarmee een zadenmengsel kan worden samengesteld dat kan worden gebruikt voor de inzaai na de dijkverbetering. Het effect van inzaai met een lokaal gewonnen zadenmengsel is zowel afhankelijk van de samenstelling van de bronvegetatie als van het moment van zaadwinning. Zadenmengsels met een aanzienlijk aandeel van *Lolium perenne* (Engels raaigras) belemmeren de vegetatie-ontwikkeling en zijn daarom ongewenst. Dergelijke mengsels dienen niet te worden toegepast, zeker niet in de hoge inzaaidichtheden van 70 à 80 kg per ha die vaak worden gehanteerd. Inzaai van eenjarige grassoorten zoals *Lolium multiflorum* of van het standaard inzaaimengsel D1 in een lage dichtheid van 20 tot 25 kg per ha lijken de vegetatie-ontwikkeling niet te belemmeren.

Acht-en-negentig procent van de plantensoorten die zijn aangetroffen voor de dijkverbetering is ook na de verbetering teruggevonden. De meeste soorten zijn opnieuw aangetroffen op de teruggezette oorspronkelijke toplaag. Slechts enkele (zeldzame) soorten zijn niet teruggekeerd op de verbeterde dijk maar hebben zich alleen weten te handhaven in de gespaarde zone. De meeste min of meer zeldzame soorten blijken na de dijkverbetering slechts in lage aantallen voor te komen waardoor de kans bestaat dat ze alsnog verdwijnen, zeker wanneer geen goed beheer wordt toegepast. Vanwege deze dreiging biedt toch een gespaarde zone de beste garantie voor het behoud van soorten na de dijkverbetering.

In de eerste jaren na de dijkverbetering wordt de vegetatie vooral beïnvloed door de methode van aanleg en de inzaaimengsels. In deze periode heeft de vegetatie een relatief open structuur waardoor de concurrentie tussen de soorten laag is. Wanneer de vegetatie zich sluit neemt de concurrentie toe. Vervolgens kan het beheer van de vegetatie worden gebruikt om de concurrentie tussen de soorten te sturen waardoor ook de soortensamenstelling wordt beïnvloed. Een soortenrijke vegetatie ontwikkelt zich alleen bij een juist beheer.

Behalve door de bodemsamenstelling en de voedingsstoffenhuishouding in de bodem wordt de de soortenrijkdom ook bepaald door de bovengrondse biomassa. In het algemeen leidt een lagere biomassa tot een hogere soortenrijkdom. De bovengrondse biomassa wordt sterk bepaald door het beheer van de vegetatie. In 1994 was de soortenrijkdom bij tweemaal maaien met afvoer van het maaisel het hoogst van alle beheersvormen en was de biomassa op-twee-na het laagst.

Tweemaal maaien met afvoer van het maaisel levert de hoogste erosiebestendigheid zoals in dit onderzoek is gemeten. De holheid van de zode en de bedekking door de vegetatie zijn bij dit beheer vrijwel even hoog als bij de vier methoden van begrazing die in dit onderzoek zijn toegepast. In het algemeen is bij begrazing de holheid van de zode het laagst en de bedekking door de vegetatie het hoogst, direct gevolgd door tweemaal maaien met afvoer van het maaisel. Daar staat tegenover dat bij tweemaal maaien met afvoer de worteldichtheid en met name de wortelverdeling beter is dan bij begrazing.

Op basis van de eigenschappen van de vegetatie die van invloed zijn op de erosiebestendigheid van de grasmat, zoals holheid van de zode, bedekking door de vegetatie, doorworteling en afschuifweerstand, blijken de beheersvormen beweiden in juni in combinatie met maaien in september, maaien in juni in combinatie met beweiden in september en tweemaal maaien met afvoer het beste te voldoen. In dit opzicht zijn ook wisselbeweiding, seizoenbeweiding, eenmaal maaien met afvoer in september en tweemaal maaien met afvoer in juni en zonder afvoer in september redelijk goede beheersvormen. Eenmaal maaien in juni, tweemaal maaien zonder afvoer, eenmaal maaien per twee jaar, branden en geen beheer zijn slechte beheersvormen.

Op basis van ecologische gegevens als soortenrijkdom en aantal en aandeel van zeldzame soorten blijkt tweemaal maaien met afvoer het beste te voldoen. Ook tweemaal maaien met afvoer in juni en zonder afvoer in september, eenmaal maaien in juni, eenmaal maaien in september (beide met afvoer van het maaisel) en maaien in juni in combinatie met beweiden in september blijken in dit opzicht redelijk goede beheersvormen te zijn. De overige vormen van beweiding, maaien zonder afvoer, eenmaal maaien per twee jaar, branden en geen beheer hebben een negatieve invloed.

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CURRICULUM VITAE

Cyril liebrand werd geboren op 28 mei 1958 te Zundert. Hij behaalde het VWO diploma (Gymnasium ß) in mei 1976 aan het Sint Thomascollege te Venlo. Aansluitend startte hij de studie Biologie aan de Katholieke Universiteit in Nijmegen. Tijdens de doctoraalstudie doorliep hij als hoofdvak Geobotanie waarbij hij onderzoek deed op Terschelling en in Zeeland en als bijvakken Biogeologie en Natuurbeheer, laatstgenoemd vak aan de Landbouwuniversiteit in Wageningen. Het laatste onderdeel van zijn studie betrof het behalen van de 1e-graads onderwijsbevoegdheid.

Van medio 1984 tot eind 1985 vervulde hij de vervangende dienstplicht als gewetensbezwaarde bij de Provincie Gelderland. Gedurende deze periode werkte hij als inventarisatiemedewerker mee aan de kartering van de provincie Gelderland en werkte hij mee aan het Veiligstellingsplan natuurgebieden van dezelfde provincie.

Van eind 1985 tot medio 1987 volgde een aanstelling aan de vakgroep Vegetatiekunde, Plantenoecologie en Onkruidkunde van de Landbouwuniversiteit in Wageningen. In deze periode werd een, eerder door de vakgroep begonnen, onderzoek naar de natuurtechnische en civieltechnische aspecten van rivierdijken in het oostelijke rivierengebied afgerond. Tussen medio 1987 en eind 1990 volgde een nieuwe aanstelling bij dezelfde vakgroep. In deze periode werd een grootschalig experimenteel onderzoek opgezet waarin verschillende facetten van dijkaanleg en dijkbeheer werden beproefd. De eerste fase van het onderzoek werd in 1990 afgesloten met een uitgebreide tussenrapportage waarin met name de kortetermijnaspecten van de dijkaanleg aan de orde kwamen. Van begin 1991 tot eind 1995 volgde een nieuwe aanstelling. In deze periode werd op de eerder genoemde experimentele dijk een tweede fase van het dijkonderzoek uitgevoerd waarbij met name de langetermijnaspecten van het dijkbeheer werden onderzocht.

Op 1 maart 1996 startte hij zijn adviesbureau EurECO dat zich richt op ecologisch onderzoek en advies. Binnen dit kader verricht hij momenteel onderzoek voor en geeft hij adviezen aan diverse waterschappen, met name op het gebied van dijkverbetering en dijkbeheer. Naast deze activiteiten doet hij onderzoek voor en geeft hij adviezen aan overheidsinstellingen, natuurbeschermingsorganisaties, bedrijven, belangengroeperingen en particulieren, steeds met het doel de natuur in Nederland te ontwikkelen en te behouden.